ORNAMENTS AND OVERFLIGHT BEHAVIOUR OF TUFTED PUFFINS (*FRATERCULA CIRRHATA*) BREEDING ON TRIANGLE ISLAND, BRITISH COLUMBIA

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Abstract

Tufted puffins (*Fratercula cirrhata*) are unusual among seabirds in that they bear multiple colourful ornaments during the breeding season. They also engage in colony overflights when approaching the colony with food for their chicks. In this thesis I investigate the function of these traits since neither one makes any obvious direct contribution to their reproductive success

Ornaments may serve as displays for gaining mates. Theory predicts that such traits should vary more than non-display traits. I found that tufted puffin ornaments were only slightly more variable in length than non-display traits and they exhibited low length and hue variation compared to putative display traits in other species. Males possessed redder skin traits than females, but variation was similar between sexes. The signalling potential of these ornaments therefore appears low, although it may be realized through detailed mate inspection. Alternatively, other display components such as behaviour may provide display variation during mating interactions. Attributes of the various ornaments were generally uncorrelated in magnitude within individuals, suggesting that any information the ornaments contain is unique between them. No ornament measure predicted condition (size-controlled body mass).

Overflight behaviour of food-bearing tufted puffins might mitigate the risk of kleptoparasitism by gulls. Overflights were correlated with ecological variables (wind, puffin arrival rate, slope, gull presence, and gull pursuit activity) in the manner expected of evasive behaviour, but were positively correlated with kleptoparasitism events when these variables were statistically controlled for. Overflights therefore do not appear to mitigate kleptoparasitism risk, although assessing the role of overflights in kleptoparasite evasion may require an understanding of the individual context for this behaviour, as well as the association between individual overflights and gull pursuit intensity. We need to determine the costs to puffins of potential evasive behaviour before we can clearly evaluate the effect of kleptoparasitism on puffin reproductive success.

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1. General Introduction

The rich seabird community at Triangle Island, B.C., provides a unique opportunity to learn about the biology and interactions of its members. This thesis examines two aspects of the breeding biology of tufted puffins (*Fratercula cirrhata*). In order to provide the reader with a context for my research, I will begin with a description of Triangle Island and its largest satellite island, Puffin Rock, and a summary of the breeding ecology of tufted puffins at this location.

Tufted puffins belong to the Alcidae, a family of 23 species of northern hemisphere seabirds that include murres (*Uria* spp.), guillemots (*Cephus* spp.), auklets (*Ptychoramphus aleuticus*, *Aethia* spp.), murrelets (*Brachyramphus* spp., *Synthliboramphus anciens*), razorbill (*Alca torda*), dovekie (*Alle alle*), and three other puffin species (*Fratercula* spp., *Cerrorhinca monocerata*). All members of this family are aerial but have a stout body form with compact wings adapted for aquatic pursuit foraging. During winter, tufted puffins are distributed across the northern Pacific Ocean living an entirely pelagic life. For 3 to 4 months between February and October, they gather to breed at various colonies along the northern Pacific coast between Japan and California. Breeding colonies are typically located on slopes adjacent to the ocean, in locations that are free from terrestrial predators and within proximity to productive foraging areas (Gaston and Jones 1998; Piatt and Kitaysky 2002). Although tufted puffins are known to nest in rocky crevices and even human-made cavities (Wehle 1980), soil is the most common substrate for the nesting burrows. Triangle Island fulfills these criteria and each spring up to 25 000 pairs of tufted puffins breed at this site (Rodway et. al. 1990).

Site description

Triangle Island (50°52′N,129°05′W) is located at the tip of the Scott Islands chain, about 45 km northwest of Cape Scott, Vancouver Island. The edge of the continental shelf lies about 40 km further west, and is subject to upwelling by the California current during the spring and summer. The waters at the shelf edge provide an important foraging area for several local species of breeding seabirds (Triangle Island Research Station, unpublished data). Triangle Island and the satellite islands around its shoreline consist primarily of uplifted basaltic material, forming plateaus with steep slopes or cliffs around their perimeters. It is about 1.5 km^2 in area and reaches a height of 210m. Its largest satellite island, and the location of the present study, is Puffin Rock. The approximate area and height of Puffin Rock is 0.03 km^2 and 150m, respectively. The flora of both islands is dominated by salmonberry (*Rubus spectabilis*) inland, and tufted hairgrass (*Deschampsia caespitosa*) on the slopes and plateau edges. Other seabird species breeding on these islands include pelagic cormorants (*Phalcrocorax pelagicus*), Cassin's auklet (*Ptychoramphus aleuticus*), rhinoceros auklets (*Cerorhinca moncerata*), pigeon guillemots (*Cephus columba*) glaucous-winged gulls (*Larus glaucescens*), common murres (*Uria aalge*), and Leach's storm petrels (*Oceanodroma leucorhoa).* The islands also feature several active bald eagle (*Heliaeetus leucocephalus*), peregrine falcon (*Falco peregrinus*), northwestern crow (*Corvus caurinus*) and common raven (*Corvus corax*) nests.

Tufted puffin breeding ecology at Puffin Rock, Triangle Island

Tufted puffins usually arrive at Triangle Island in April and spend the first few weeks showing intermittent offshore attendance. They begin visiting the breeding slopes in flocks by mid to late April. Slope settlement begins with general attendance of one to several days at the colony, followed by an absence of one to several days, as has been reported in other alcid species at different sites (Gaston and Jones 1998).

Breeding display behaviour is evident from the earliest slope attendance, and increases as slope attendance becomes regular. Display behaviour includes paired flights and landings at burrow entrances, mutual side-to-side head wagging with contact between bills, allo-preening, burrow issuing, guided burrow tours, aggressive displays toward intruders, and general displays such as head shakes, tuft flares, and stationary wing flapping (Wehle 1980; GSB, pers. obs). Some displays (e.g. wing flapping and headshakes) also occur on the water, which is the site for copulation (GSB, pers. obs.). It is perhaps a combination of interactions on the water combined with initial burrow attendance and displays on the slope that creates the pair bond between new or reuniting mates. Tufted puffins are monogamous but there is currently no data on divorce rate or extra-pair copulation rate (Gaston and Jones 1998). During the courting period, a persistent slope-attendance pattern develops that is characterised by highest surface attendance during the early morning, and late afternoon to evening (Gjerdrum 2001; GSB, unpublished data).

Egg hatch data indicates that most egg laying occurs within the first two weeks of May (Triangle Island Research Station, unpublished data; Gjerdrum 2001; GSB, unpublished data). Clutch size in this species is one egg. No quantitative data exist for activities within burrow, so patterns of nest attendance following egg-laying are unclear. Consistently warm eggs and high frequency of attended eggs during burrow checks suggest that egg attendance is probably quite regular (GSB, unpublished data). Adult Atlantic puffins have been reported to share roughly equally in incubation and food-provisioning of chicks (Creelman and Storey 1991). It appears that many of the tufted puffins on the colony surface during the egg-laying and incubation phase are breeders trading off incubation shifts and simply remaining at their burrow entrances (GSB, pers. obs), rather than immediately departing to sea.

Incubation lasts about 45 days (Triangle Island Research Station, unpublished data; Wehle 1980), so peak hatch usually occurs between mid June and early July. When the nestling phase begins, parents share in brooding and delivering food to chicks, with peak deliveries occurring during the early morning and mid to late evening (Gjerdrum 2001; Cassady St. Clair et. al. 2001; GSB, unpublished data). Parents deliver loads predominantly composed of sandlance (*Ammodytes hexapterus*) at a rate of about 4-5 deliveries per day during relatively successful seasons (Gjerdrum 2001). Other prey species include rockfish (*Sebastes* spp.) and squid (*Loligo* spp.), with low frequencies of other small fish and invertebrates (Vermeer 1979; Gjerdrum 2001, GSB unpublished data). In contrast to the brief nestling period in non-puffin species of alcids of comparable size (about 3 weeks in *Alca torda* and *Uria* spp. [Gaston and Jones 1998]), nestling development in tufted puffins takes from about 45-55 days, allowing chicks to gain between 350-500g (between about 50-75% of adult mass) and a full set of flight feathers prior to nest departure (Vermeer and Cullen 1979; Gjerdrum 2001; GSB, unpublished data). Fledging at Puffin Rock peaks in mid August and ranges from late July to early September.

Surveys conducted since the 1970s indicate that tufted puffin annual breeding success at Puffin Rock varies between about 3-81% fledglings per egg laid (Vermeer et. al. 1979; Gjerdrum 2001, Cassady St. Clair et. al. 2001; GSB, unpublished data) and is at the low end of this range for 3 to 4 out of every 5 years (Triangle Island Research Station, unpublished data; Gjerdrum et. al. 2003). Although the reasons for these fluctuations are poorly understood, decreased proportions and size of sandlance in the food loads of chick-rearing parents appear associated with abandonment by adults, low chick growth rates, and high chick mortality (Vermeer et. al. 1979; GSB, unpublished data). It has therefore been suggested that shortages of this primary prey species may play a proximate role in the breeding failures (Vermeer et. al. 1979; Gjerdrum et al. 2003).

Research topics

Tufted puffins exhibit some unique features that, in combination with their relatively frequent breeding failures, make them both an intriguing research subject and a species of conservation concern. In the current thesis, I focus on two of these features. The first concerns the potential signal value of their breeding ornaments. Several of the puffin and auklet species are relatively ornate during their breeding seasons compared to other seabirds. Elaborate display traits are often demonstrated to be under selection by prospective mates or competitors for mates (Andersson 1994), and can therefore teach us about signal strategies and individual qualities of their bearers. I measured ornaments of a sample of tufted puffin adults in June to investigate whether their feather and skin ornaments 1) vary to the extent expected of putative sexually selected traits (greater than non-ornamental puffin traits, and to a similar degree as other species) 2) differ between sexes 3) correlate in magnitude with each other, and 4) correlate with one measure of body condition.

My second research topic concerns the flight behaviour of puffins as they approach the colony to deliver food to their chicks. Colony overflights are exhibited by several species of alcids, and are thought to play a role in both intra-specific social interactions and avoidance of predators and kleptoparasites (e.g. Taylor 1982). Among puffins that approach their colony under risk of being either robbed or preyed upon, overflights appear intended to help individuals evade attacks by their pursuers. Interpretations of the evasive function of overflights are hindered by other ecological factors that may also covary with this behaviour. Puffins at Puffin Rock breed in proximity to hundreds of glaucous-winged gulls, and consequently provision their chicks under kleptoparasitism risk (Cassady St. Clair et. al. 2001). My goal was to examine variation in overflights with respect to kleptoparasitism while controlling for other prominent ecological features associated with these events.

2. Natural variation in tufted puffin breeding ornaments

Introduction

Many species exhibit conspicuous morphological and behavioural traits during their breeding season. Classic examples are elaborate horns of ungulates, and plumage, flight, and song displays of birds. Darwin (1859, 1871) noted that breeding display traits often appear to pose survival costs (e.g. diminished foraging ability, increased predation risk), and he suggested that such traits are designed by a struggle for mates rather than survival. He distinguished 'sexual selection' as a special form of natural selection that shapes breeding displays through the differential reproductive success of their bearers. Evidence now exists among diverse taxa that bearers of relatively well-developed displays gain reproductive advantages through increased attractiveness to the opposite sex (widowbirds [Andersson 1982]; red junglefowl [Zuk et. al. 1990]; yellowhammers [Sundberg 1995]; guppies [Brooks and Endler 2001]; wolf spiders [Parri et. al. 2001]) or increased success during intrasexual competitions for mates (red deer [Clutton-brock 1982]; auklets [Jones 1992]; fiddler crabs [Hughes 1996]; Gambel's quail [Hagelin 2002]).

In many cases, the ultimate basis for receiver preferences appears to be the utility of displays as signals of fitness benefits (Darwin 1859, 1871; Fisher 1915, 1930; reviewed in Andersson 1994). Displays can reflect immune system function (Duufva and Allander 1995; Saino et. al. 1999), body parasites (Fitze and Richner 2002), body condition (Hill 1994; Saino et al 1997; Kotiaho 2000), parental quality (Hill 1991; Voltura et. al. 2002), and can also predict offspring quality (Norris 1993; Johnsen et. al. 2001). Since signals are affected by historical, ecological and developmental constraints (Badyaev and

Qvarnstrom 2002; Badyaev and Hill 2003), they can also inform us of the role of such constraints in shaping signal strategies. Selection acting on breeding displays is gaining recognition as a potentially important factor in processes of population divergence (Uy 2000; Boughman 2001; Podos 2001; Masta and Maddison 2002). These findings indicate that research on the signalling function of breeding display traits offers important insights not only to the forms we observe in nature, but also to the processes that determine their distribution.

Among seabirds in the northern hemisphere, most species of puffins (*Fratercula* spp.) and the closely related auklets (*Aethia* spp.) are unique for their high degree of breeding ornamentation. Breeding tufted puffins (*Fratercula cirrhata*) of both sexes possess a long yellow tuft of feathers above each eye, a white plumage patch across the entire face, a massive bill covered by several red keratinised plates and a yellow basal cere, a fleshy red rosette at each corner of the mouth, red eye rings, and red legs and feet. The purpose of this study was to document tufted puffin ornamentation and evaluate several aspects of ornaments that are of pertinence to their role as breeding signals.

Display traits under current sexual selection typically exhibit greater variation than traits that are important for individual survival such as body structure (e.g. Darwin 1859; Alatalo et. al. 1988; Møller and Pomiankowski 1993). This variation is probably central to their utility as signals between individuals (Krebs and Dawkins 1984) and forms the basis for models of sexual selection (reviewed in Andersson 1994). In this study, I compared variation in ornament length to variation in the length of structural traits (tarsus, culmen, and wing chord) as a means of identifying whether the ornaments appear to be under sexual selection. I also measured ornament hue to quantify hue variation for comparison with putative sexually selected traits in other species.

Females are generally considered to be more selective about mates than are males because females are constrained in reproductive success by embryo development and often an unequally large share in the care of offspring. This imposes greater selection pressure for display on males and is reflected in male displays of relatively greater magnitude. In cases where ornaments are costly to bear, ornaments of greater magnitude are expected to be more variable due to the differential abilities of bearers to pay the costs of ornamentation. In puffins, the large investment required to raise a single chick is shared between parents (Gaston and Jones 1998; Piatt and Kitaysky 2002), but females are still constrained to raising one chick per season while males can potentially sire more than one offspring. Consequently, I compared ornaments between sexes, predicting that if any difference existed between the sexes it would be through greater ornament magnitude and variance in males.

I also examined patterns of correlation among the ornaments in order to evaluate the nature of their potential signalling function. Møller and Pomiankowski (1993) outlined three hypotheses to distinguish the potential signalling functions of multiple ornaments: the "redundant message" hypothesis predicts that ornaments are highly correlated and consequently function as a single display; the "multiple messages" hypothesis predicts they vary independently and each contains unique information about their bearer; and the "uninformative" hypothesis predicts the ornaments contain no decipherable information at all. Both of the latter hypotheses predict lack of correlation among ornaments. I assessed support for the first versus second two of these hypotheses by determining if the ornaments are correlated in hue and size.

Finally, I compared ornamentation to an index of body condition. Body size-corrected body mass is a mass measure that controls for the allometry in mass among individuals of different structural sizes. This condition measure is assumed to reflect the extent to which individuals possess beneficial body reserves such as fat and muscle tissue (Schulte-Hostedde et. al. 2001; but see Green 2001). I predicted that if ornaments signal information about adult foraging ability or general health, ornament magnitude would be positively correlated with body condition.

Methods

Trapping and measurement protocol

Fieldwork was conducted on the colony at Puffin Rock, Triangle Island (B.C.), during eleven days between May 29 and June 30, 2002. Trapping sessions were typically about 6 hours in length, either following dawn or prior to dusk, but full-day sessions were conducted on four days of very low slope attendance. Puffins were trapped using nooses made from 30lb gauge plastic monofilament line, which was thick enough to restrain adults without cutting the skin on their legs. Nooses barely large enough to fit the foot of an adult puffin were secured about every 5cm along 20cm lengths of cord, resulting in noose cords with 4 to 6 nooses each. Noose cords were pegged in front of the burrow entrance with several aluminium tent pegs so that individuals entering or leaving the burrow, or walking near the entrance, might step into a noose. Noose cords were highly effective at capturing adults and easy to remove. All materials were in drab colours since bright colours deterred puffins from approaching the traps. Up to thirty traps were set per trap session and monitored continually with binoculars from a distance. Trapped birds were detected immediately once they stepped into a trap and began to struggle. They were removed from traps within about 3 minutes from capture and transported back to the observation blind secured in an opaque, ventilated bag. The handling time of each individual was about 20 minutes, and individuals waiting to be processed were stored within their bags in ventilated, shady conditions. No bird was detained for more than 60 minutes. Of 153 puffins that have been captured using this protocol at Triangle Island, one bird died in detention while awaiting processing. The remaining 152 subjects appeared unharmed and typically flew vigorously upon release. Sixty-nine of these adults were captured during the present study in June 2002, including 40 females and 29 males.

Each individual was fitted with a numbered stainless steel leg band on the right leg, and a three-colour combination of plastic leg bands. Colour bands have been shown to influence mate choice in other studies (e.g. Gratson et. al. 1991; Swaddle 1996) so I assigned unique, randomly selected, asymmetrical colour combinations to each bird, in an effort to minimize and randomise this effect at our site.

Sexing individuals

A blood sample of 1cc was drawn for molecular sexing purposes. Birds were later sexed in the laboratory following the methods of Fridolfsson and Ellegren (1999).

Morphological measurements

We recorded subject mass and the length of several non-ornamental (flattened right wing chord length, right tarsus length, culmen length, head-plus-bill length) and ornamental (bill depth from the base of the upper cere to the lowest dip in the lower mandible, upper cere edge length, right tuft length from origin over eye to tip) traits. A single observer (GSB) made all of the measurements.

Photographs

Photographs were made using the manual function with standardized light and speed settings of a Sony Cyber-Shot 4.2 mega pixel digital camera. Individuals were photographed in a standardized pose against a wooden apparatus, within a light-sealed observation blind. For each bird, a photograph of the right and then left side of the face was taken, as well as a third photograph of their right foot.

Ornament colour sampling

Digital photos were transferred to a Dell Inspiron 1100 computer and imported into Adobe Photoshop 6.0 (Microsoft Corp.) for colour sampling. Patches of colour were sampled by outlining standard areas within each ornament. Ornaments sampled were upper mandible (anterior, middle, and posterior plates) and lower mandible, gape rosette, eye ring, cere, tuft, foot web, and toe. I derived estimates for colour by firstly using the Adobe 'histogram' function to calculate the intensity of red, green, and blue components for each patch. These components were entered into the 'colour picker' function to calculate hue (measured as a position on a 360° colour wheel), saturation (proportion of hue with respect to grey, from 0-100%), and brightness (relative lightness, from 0-100%).

Sampling errors in hue, saturation, and brightness between photographs were controlled for by comparing to a yellow reference chip in each photograph. The range of variation across all subjects was less for ornament than chip colour, indicated by regressions of ornament on chip colour having absolute slope values of less than 1.00 (except toe slope = 1.02; GSB, unpublished data). This indicates that the chip was more sensitive to photograph colour error than ornaments, suiting it to its role as a colour standard. Residuals of hue, saturation, and brightness measurements for each ornament were derived from regressions against their respective yellow chip, and these residuals were used for all subsequent analyses of ornament colour.

In order to confirm the reliability of the colour sampling protocol, I evaluated repeatability of colour measurements by comparing colour measurements from photos of the left and right facial aspects of individuals (duplicates of the same facial aspect were unavailable). This provides a conservative assessment of repeatability since slight natural variation in colour is expected between aspects of each individual. Yellow colour standard chip hues were highly repeatable among photos ($r^2 = 0.80$, $F_{1,64} = 264.1$, $p < 0.0001$). Residuals of ornament hues against the colour standard were strongly correlated (Table 2.1). Duplicate photos of webs and toes were unavailable for analysis. I assumed hue values were highly repeatable for these traits, as demonstrated for the other red skin traits. This assumption is substantiated by narrow variation of leg hue (see Results).

Saturation and brightness were excluded from analyses since these measures were highly variable among repeated samples within photos. No colour analyses were conducted for the white face patches, nor for the black body plumage, because initial measurements indicated that all colour components for these traits were highly variable among repeated samples within photos.

Preliminary analyses indicated that the four bill hue and two leg hue measurements each correlated with one another, so I derived principle components to represent these traits. PC1 for the four bill measurements ("bill") weighted each measurement roughly equally (between 0.47 and 0.54), and explained 72.5% (females) and 80.1% (males) of their variation. PC1 for the two leg measurements ("leg") weighted each measurement equally (0.71), and explained 70.9% (females) and 89.3% (males) of their variation.

Structural body size was estimated for each individual in order to derive body condition estimates and to examine the potential role of body size in ornament variation. Principal components were derived for measurements of tarsus and head-plus-bill length. PC1 loaded each variable equally (0.71) and explained 73.9% of the variation in these data. Residuals of body mass on body size or ornament length on body size were used as indices of body condition and size-corrected ornament length, respectively.

Statistics

Statistics were calculated using JMP 4.0 (SAS Institute). Levene's test was used to test differences in variance between sexes. Differences in ornament length and colour measurements were tested between sexes using t-tests, or Welch's test in the case of unequal variances among samples. Measurements were correlated using linear correlation and the multivariate correlation platform in JMP 4.0. Power calculations for correlation coefficients were made with Power and Precision software. Re-sampling of ornament data to create theoretical distributions of correlation coefficients was conducted using Excel Add-in 2.0 (Resampling stats) in Excel 2000 (Microsoft Corp.).

Results

Variation in ornament size and hue

Ranges of lengths across both sexes were: right tuft (93-125 mm); bill depth (41.0-48.9 mm); cere (22.5-31.5 mm); tarsus (34.6-39.8 mm); culmen (50.8-63.7 mm); flattened wing chord (197-221 mm). Ornaments increasing significantly with body size were bill depth (females: slope = 0.882, $r^2 = 0.303$, $F_{1,37} = 15.7$, $p = 0.0003$, males: slope = 0.608, $r^2 = 0.213$, $F_{1,28} = 7.3$, $p = 0.01$) and cere (females: slope = 0.788, $r^2 = 0.176$, $F_{1,37} = 7.7$, $p = 0.009$, males: slope = 0.776, $r^2 = 0.267$, $F_{1,28} = 9.9$, $p = 0.004$), while tuft length and all ornament hues showed no significant relationship ($p > 0.15$). It is unknown whether or not ornament lengths signal information that depends on body size. I therefore examined variation for both absolute and body-size corrected ornament lengths. Body-size corrected ornament lengths were derived from a general linear model that controlled for body size. Coefficients of variation were used to compare ornament size variation in order to control for differences in variation expected solely due to differences in the size of different structures,. Individual coefficients of variation for all ornament lengths were greater than those for non-ornamental traits, except for female bill depth (Table 2.2a). The mean coefficient of variation for three absolute ornament lengths was significantly greater than that for three non-ornamental lengths in males but not females. The difference was statistically significant when sexes were pooled (Table 2.2b). Similarly, the mean coefficient of variation for three body size-corrected ornament lengths was significantly greater than that for three non-ornamental lengths in males but not females (Table 2.2a). This difference was not statistically significant when sexes were pooled (Table 2.2b). Overall, ornament length variation tended towards slightly greater than that of non-ornamental traits, but the difference was statistically significant only in males.

Non-ornamental hue variance measurements were unavailable for comparison with ornamental hue variance. Hue variation was low for all ornaments measured. Standard deviation in hue across all traits ranged between 1-5° on a 360° colour wheel when sexes were pooled or analysed separately (Table 2.3).

Sexual differences in ornamentation

Males were larger than females in the three non-ornamental traits measured (Table 2.2a). When absolute ornament values are compared, males had significantly greater bill depths than females (Table 2.2a, Figure 2.1). Males had only slightly larger bill depths and females had slightly larger ceres when body size was controlled for, although these effects were not significant at the Bonferroni adjusted α-level (0.017) for the three body size-controlled length comparisons (Table 2.2a, Figure 2.1)(Rice 1989). Variance was equal between sexes for the three length and six hue measures at the Bonferroni adjusted α-level (0.02 and 0.008, respectively), although male tuft hue variance approached a significantly higher value (Levene's test; $F_{1,64} = 6.05$, $p = 0.017$). Legs, rosettes, and eye rings were redder in males than females (Table 2.3a, Figure 2.2). Ceres were slightly more yellow in females, although not significantly so at the sequential Bonferroni adjusted α-level (0.017) for this comparison. Hence, several ornaments supported the prediction of greater ornament magnitude in males, but no trait supported the prediction of greater variance in males.

Correlations among ornaments

Based on absolute ornament lengths, bill depth and cere length were highly correlated in both sexes (Table 2.4). Leg and bill hue were correlated in males but this result was not significant at the sequential Bonferroni adjusted α-level (0.001) for this comparison. Other marginal correlations (female ring and tuft hues, male bill hue and bill depth, and male tuft hue and tuft length) were not significant following Bonferroni adjustments. The results were qualitatively similar when body size-controlled ornament lengths were substituted in the analysis, except the marginal correlation between male bill hue and bill depth was not significant ($r = -0.362$, $p = 0.06$), and correlation between female cere length and bill depth was not significant ($r = 0.387$, $p = 0.02$) at the table wide alpha level. The strength of the actual relationship required to detect significant pair-wise correlations with power = 0.80 was $r = 0.38$ for females ($n = 39$) and $r = 0.43$ for males ($n = 29$) within each analysis. Ornaments were in general uncorrelated, providing support for the idea that the ornaments are either uninformative, or that each one contains unique information.

It is possible that there is a significant positive relationship among ornaments when all are considered together, rather than on a pairwise basis. I therefore also asked whether the number of positive r-values observed across all comparisons for each sex were likely to occur by chance in the absence of a significant positive relationship among ornaments. I bootstrapped the ornament measures to generate 10 000 correlation matrices for each sex, representing random associations of ornament values. I recorded the positive r-value counts for each matrix, and then compared the observed positive r-value count for each sex to their respective null distribution of positive r-value counts. The outcome of this analysis is subject to the directions of the pairwise relationships between traits. Care is therefore required in deciding what constitutes greater magnitude for each trait. The red ornaments probably increase in magnitude toward greater red values and the yellow tufts increase toward yellow, as has been demonstrated for other red (Zuk et. al. 1990; Eens et. al. 2000) and plumage ornaments (Hill 1991). The status of the cere as an ornament was unclear, since it varies within both the red and yellow range of the spectrum, appears translucent, and potentially has a role in development of the red bill sheaths. I assumed that ceres increase toward yellow, since that appears to be the hue of the material composing the cere itself. Further information is needed about the physiological basis of colouration in all of these ornaments. Observed positive r-value counts using absolute ornament lengths were: (females) 21/36, $p = 0.20$, (males) 20/36, $p = 0.31$, (pooled) 23/36, $p = 0.07$. These results indicate that ornaments vary independently both on a pairwise basis and when considered collectively. The analysis was not repeated for body size-controlled ornament lengths, given the similarity in results for pairwise correlations involving these data.

Ornament magnitude and body condition

A composite trait score was included in this analysis in order to assess whether all traits together predict body condition. The uncorrelated ornament hues and lengths (above) prevented effective use of a principal component to represent this score. Consequently, I ranked each ornament magnitude within the range of values observed across all puffins for that trait, and then summed the ranks for each individual. Using absolute ornaments lengths in the analysis, body condition did not significantly correlate with ornament magnitude at the Bonferroni adjusted α-level for ten comparisons for each sex (0.005), although male tuft hue was significant at α-level = 0.05 and the male composite trait score approached significance (Table 2.5). Results were also not significant when sexes were pooled, but eye ring hue approached significance. Tablewide positive r-value counts were not more common than expected by chance (females: 7/10, p = 0.17; males: 3/10, p = 0.83; pooled: 6/10, p = 0.62). Using body size-controlled ornament lengths in the analysis, body condition did not significantly correlate with ornament magnitude at the Bonferroni adjusted α-level (0.005) for ten comparisons for each sex, although male bill depth approached significance. The results were also not significant when sexes were pooled, except bill depth was significant at α-level = 0.05. In general, ornament magnitude was not correlated with the body condition index, providing no support for the hypothesis that ornaments contain information about individual general condition.

Discussion

Below, I discuss variation in tufted puffin ornaments with respect to information from other taxa and competing models of sexual selection. Several differences between the sexes in ornament magnitude support the idea that males and females are under different selection pressures or able to respond to different degrees to these pressures, and also support the idea that the ornaments have signalling value despite their minimal variation. Ornament magnitudes were not correlated in either sex, suggesting they contain either no information or discrete information. Body size-controlled body mass was not correlated with any ornament measure.

Ornament variation

Tufted puffins in this population exhibited low variation for the breeding display variables measured (Table 2.2, 2.3). Coefficients of variation for the absolute lengths of tufts and the cere were between 6.9-7.3% across all adults, compared to coefficients of 2.3-3.9% for several non-ornamental morphometric traits. Bill depth, though increasing drastically during the breeding season (Gaston and Jones 1998; Piatt and Kitaysky 2002), had a coefficient of variation similar to non-ornamental traits (3.5-3.7%). Overall, ornaments were significantly more variable than non-ornamental traits in males but not females. When data was pooled across sexes, variation was greater in absolute but not size-corrected ornaments. In contrast, research on other species indicates that sexually selected traits often exhibit large variation relative to traits under viability selection. Jones (1992, 2000) reports coefficient of variation values of between 13-16% for comparable bilateral feather ornament lengths in the closely related crested (*A. cristatella*) and whiskered (*A. pygmaea*) auklets, and 20-21% for their bill ornament (a rictal bill plate in the former and a knob on the dorsal edge of the bill in the latter), compared to about 3.5-5.5% variation in non-ornamental traits. Similarly, across more distantly related avian taxa, coefficients of variation for length or area of various feather ornaments typically range between 10-24%, compared to non-ornamental trait length measures of 1-6% (Alatalo et. al. 1988; von Schantz et. al. 1989; Zuk et. al. 1990; Møller and Pomiankowski 1993; Moller and Petrie 2002; Hagelin 2002; but see Hagelin 2002 [7.5% in non-ornamental tail feather length variation in scaled quail]; Zuk et. al. 1990

[88.2% variation in one of two samples of ornamental tail feather length variation in red jungle fowl]). Reports of colour variation are rare in the literature and comparisons are hindered by incompatible sampling methods. Hue variation is often great enough to be reliably sampled by the human eye (e.g. Zuk et. al. 1990, Hill 1992; Dufva 1995; Omland 1996; Bortolotti et. al. 1996; but see Kodric-Brown and Brown 1984), although this might reflect a research bias toward relatively variable species. In the present study, tufted puffin hue differences between individuals were virtually indiscernible to human observers, with a digitally measured standard deviation of only 1-5° on a 360° colour wheel scale. My results are probably a good representation of within-season variation in this population since trapping was conducted over several weeks on two different slopes on Puffin Rock and juveniles were among those present on the slopes during this period. No obviously different adult phenotypes have been observed at other parts of the colony, or in other years (GSB, pers. obs.).

Popular models of mate choice suggest that display signals will be variable, and the models have received widespread empirical support in this respect. "Quality indicator" models of sexual selection suggest that viability selection opposes the elaboration of costly traits, such that display variation arises due to the differential ability of individuals to pay the costs of display development or maintenance (Williams 1966; Zahavi 1975). Costly traits therefore reflect direct (e.g. condition, foraging ability) or indirect (e.g. disease resistance) aspects of parental quality that can be evaluated by choosers. For example, feather ornaments can produce flight costs that diminish foraging success (Cuervo et. al. 1996) and migration condition (Saino et. al. 1997) and that are best borne by males in superior condition (Moller 1989). Similarly, keratinised or bony features are demonstrated to involve foraging costs to their bearers (e.g. Weissburg 1992). Costs associated with coloration are also apparent in many species (Hill 1996). The red or yellow colours of ornaments are often attributed to carotenoids, a class of plant-derived pigments that animals must ingest in their food. High plasma concentrations of carotenoids are associated with increased immune response (Saino et al. 1999; Bortolotti et al 2000), and plumage ornaments exhibit diminished hue during periods when birds are in poor nutritional condition (Hill 2000) or bearing increased parasite load (McGraw and Ardia 2003). These findings suggest that ornament coloration represents a compromise between display magnitude and other important physiological processes. Ornament pigmentation can therefore reflect both individual health and foraging success. Further, such information can be signalled over different time scales, depending on the turnover rate of the material composing the ornament (Brush 1990), or its ability to change colour (e.g. Schorger 1966). Tissue colour can change within days or weeks (J. Dale, pers. comm.), providing a current account of individual pigment or hormone levels, while pigments invested in feathers remain relatively intact until feather loss.

Other models of sexual selection do not depend on signal cost to explain the evolution of breeding display traits, although they imply costly and variable endpoints. Fisher (1930) suggested that heritable display traits may evolve simply because they are attractive to receivers, and therefore become genetically correlated with receiver preferences. The result of this scenario is a "runaway" process, in which both the display trait and the preference for it increase. However, Fisher also suggested that such traits should cease to evolve when they reach costly magnitudes (1915). A similar outcome might be achieved by "sexual antagonism" (Holland and Rice 1998). In this model, natural selection favours receivers to resist breeding signals, and favours signallers to evolve displays that overcome receiver resistance. Signallers develop a new display when further elaboration of the previous one becomes too costly in order to keep ahead of receiver choosiness, but they may also need to retain older displays in order to stimulate receivers. Consequently, traits should also reach costly magnitudes under the antagonistic process, but due to signallers of different levels of quality differentially responding to chooser resistance rather than favour.

With their variety of ornament structures, and coloration based in feather, keratin, and skin, tufted puffins possess a variety of putative display traits of comparable structure and composition to the costly traits mentioned above. Energy costs due to mass or drag of bilateral tufts and developed breeding bills may be significant in tufted puffins, particularly since they have an exceptionally high ratio of body mass to wing area among aerial species (Spear and Ainley 1997). The physiological basis of puffin ornament coloration remains to be determined, but carotenoids are likely the pigments of the red ornaments (K. McGraw, pers. comm.). Repeated capture of individuals across the entire season would be required to rigourously assess individual temporal hue variation. I observed no temporal variation across my sample, collected over four weeks in June, nor did I observe large variation expected in the hue of tufts as would be expected if tuft hue serves a non-temporal signalling function. The low hue and length variation documented in this study suggests that if information about cost is contained in tufted puffin ornament hues and lengths, it is communicated across narrow ranges of magnitude.

Selection might favour minimal variation in visible display traits if the social costs to signallers of widely advertising individual status are great. This idea has been suggested in the case of coverable display traits in situations where adult interactions are frequent and the risk of aggressive encounters provoked by ornaments is high (e.g. Hansen and Rohwer 1986; Viega 1996). Such a force might also operate in tufted puffins since adults defend burrows and display within metres of their immediate neighbours, in colonies of up to thousands of adults. The greater inspection-time required by narrowly varying ornaments might be feasible during this species' prolonged mating rituals. Mating rituals include mutual inspection (paired flights, allo-preening, posture displays, ocean surface copulation rituals [Piatt and Kitaysky 2002; GSB, pers. obs.]) behaviours that occur from one to several weeks prior to egg-laying. There might be ample opportunity in this situation to carefully inspect the individual or combined ornaments of prospective mates during these rituals, and also compare them to nearby resident adults. Display behaviour itself might also provide a large and concealable source of variation with which mate value can be judged among tufted puffins (Calkins and Burley 2003). Ornamentation has been associated with behavioural dominance in many species (Clutton-Brock et. al. 1982; Jones and Hunter 1993; Jones 1999) and in several cases display behaviour establishes dominance (e.g. Hughes 1996) and mating success (Hagelin 2002; Kodric-Brown 1993) independent of ornament magnitude. It is possible that tufted puffin ornaments play a role as relatively unvariable highlights for behavioural display. Investigations of both the social consequences of manipulated ornament magnitude (e.g. Jones and Hunter 1993) and the contribution of individual display variation to breeding success would help to examine these issues.

A related possibility to explain lack of ornament variation is that the ornaments vary in aspects that I was unable to evaluate. Saturation and brightness of ornament colours may be under sexual selection in tufted puffins, as has been demonstrated in other species (Zuk et. al. 1990; Pryke et. al. 2002; Johnsen et. al. 2003; but see Dale 2000; McGraw et. al. 2000; Fitze and Richner 2002). Measures of these colour components varied too much between photographs of the same individual to be analysed in the present study. Also, displays in many avian species reflect light in the ultraviolet ("UV") spectral range, and can signal aspects of adult quality (Keyser and Hill 1999; Siitari and Huhta 2002; Johnsen et. al. 2003; Seifferman and Hill 2003) and function in mate choice (Bennet et. al. 1996; Andersson and Amundsen 1997; Johnsen et. al. 1998; Siitari et. al. 2002; Seifferman and Hill 2003). Current information on UV perception in seabirds is limited to three species of boobies (Sulidae), in which response to this portion of the spectrum ranged from absent to strong (Reed 1987). Further work is required to determine whether saturation, brightness, and UV colour vary significantly among tufted puffins. For now, our results indicate that this species varies minimally in ornament length and in hues visible to humans, both of which are important aspects of sexually selected traits in other avian taxa (Zuk et. al. 1990; Hill 1996; Omland 1996; McGraw et. al. 2000; Hill 2000).

A final consideration is that variation in ornament expression has been constrained by a genetic bottleneck. Puffins tend to return to their natal colonies to breed (Harris 1984; Gaston and Jones 1996), and this diminishes the chance of foreign adults arriving at Triangle Island. A small founding population or a population reduction at some point in the colony's history might therefore have led to limited ornament variation. On the other hand, the dispersal distance between this site and their northern Pacific Ocean winter range is great (Piatt and Kitaysky 2002) and the colony at Triangle Island is large (~45 000 adults; Rodway et. al. 1990), suggesting that there is potential for winter interactions to occur between populations and for foreign adults to arrive at Triangle Island and breed. In this light, it appears likely that Triangle Island experiences ongoing gene flow. Further, the condition-dependent nature of similar display traits in other species (above) suggests that environmental rather than genetic control may play a primary role in determining ornament magnitude in tufted puffins. Nonetheless, a survey of genetic variation among Triangle Island puffins and also an inter-population comparison of ornament magnitude and variation would both help to clarify whether genetic variation at Triangle Island is low, and whether genetic and ornament variation are unique to this site.

Sexual differences in ornamentation

Slight sexual dimorphism was observed in the hue of fleshy traits, with males being redder in each case. This supports the prediction that males have responded more to sexual selection or have been under greater sexual selection for these traits, but it is unclear why the same pattern does not occur among all ornaments. It is possible that the red skin ornaments convey information pertaining to sex-biased breeding roles such as burrow defence or mate competition. Flesh hue has been shown to mediate behavioural interactions and mate choice in several species (Ligon and Zwartjes 1995; Hagelin and Ligon 2001; Eens et. al. 2000), and in common moorhens these traits are testosterone mediated in both sexes but more developed in males under natural conditions (Eens et. al. 2000). Jones (2000) found male-biased sexual dimorphism in size of rictal plates and auricular plumes but not in the size of crests of Crested auklets, despite the role of crests in mediating behavioural interactions in this species. Similarly, in least auklets, he observed no dimorphism in facial plumes, despite their role in mediating behavioural interactions (1992). Colour was not analysed in either study. The potential for skin and plumage ornaments in tufted puffins to affect behavioural interactions remains to be tested. The observed differences in skin traits might also reflect higher costs of pigmentation to the condition of females or their developing embryos. This idea is supported by the fact that redder male skin traits did not exhibit relatively greater variation indicative of greater costs of expression for males. Information about the different physiological roles of carotenoids between sexes is needed to thoroughly explore this possibility. This might be obtained through analyses of bloodstream carotenoid levels between sexes, and females in different stages of reproduction. Marginal levels of dimorphism were also observed toward males in bill depth and toward females in cere yellowness, body size-controlled length of the cere, and tuft variation. Although these results were not significant after Bonferroni adjustments, they suggest that these and skin traits may be under sex-specific selection, and may therefore play a role in signalling strategies of the two sexes. The differences between sexes observed in the skin trait hues further support the idea that tufted puffin ornaments in general may function as signals across narrow ranges of magnitude.

Correlations among ornaments and comparison with body condition

Ornament length and hue magnitude varied independently on a pairwise basis except for cere length and bill depth measures in both sexes, and leg and bill hue in males, although the latter result was not significant when adjustments were made for the large number of comparisons for each sex. Table-wide sign tests of correlation coefficients derived from bootstrapped data indicated no strong trend in either sex. Ornaments also tended to vary independently among multiple traits in several dimorphic species measured by Moller and Pomiankowski (1993). Schluter and Price (1993) suggested that, particularly in situations where advertising opportunity is high, ornaments may continually evolve that are increasingly informative and detectable to choosers until one arises that negates previous ones. Alternatively, multiple ornaments may be favoured in situations where signals contain diverse information (Moller and Pomiankowski 1993) or are intended for more than one type of receiver (Berglund et. al. 1996; Andersson et. al. 2002) or situation. Under either scenario, or a combination of the two, ornaments may vary independently from one another. Across species, different ornaments within ornament assemblages often correlate with different fitness parameters (Jones 1991, 2000; Badyaev et. al. 2001; Hagelin 2002; Moller and Petrie 2002; Doucet and Montgomerie 2003), suggesting that several ornaments may often contain different, current information about the genetic or parental quality of their bearers. It is also possible that ornaments signal adult identity (Dale et. al. 2001) or quality when considered collectively. The minimal variation observed across different ornaments in the present study suggests that any identity signalling function is probably weak in tufted puffins, since pure signals of identity are expected to be uncostly and vary widely (Dale et. al. 2001). Correlates of quality remain to be examined in this species; adult sensitivity to capture within our study plots and low reproductive success across the Puffin Rock colony during 2002 (GSB, unpublished data) prevented an evaluation of multiple fitness correlates. No ornaments were correlated with body condition after adjustment for multiple comparisons, although the composite measure and tuft hue in males approached significance. Our measure of body condition (body size-controlled mass) is sensitive to stomach content at the time subjects are measured, so would only detect strong relationships between mass and size. In much larger samples of least and crested auklets, Jones (1992, 2000) found only slight relationships between ornaments and body size-controlled mass. Plumage ornaments that are favoured by both sexes indicate age and social dominance in these species (Jones and Hunter 1993; Jones 1999). The complex breeding rituals employed by tufted puffins provide opportunity for signalling between both potential mates and adversaries on the breeding slopes and water, and the variety of materials represented by the ornaments indicate potential for diverse information content. These considerations, as well as the differences between sexes in covariation of bill and leg hue observed in the present study, suggest that multiple ornaments may generally serve as separate and informative signals for both male and female tufted puffins. It might be possible to observe correlations between ornament magnitude and fitness parameters during seasons with relatively high breeding success, although large samples would be required to examine ornament meaning across the narrow ranges of variation I documented.

Conclusions

Tufted puffins exhibited minimal hue and size variation across different types of ornaments that have demonstrated physical costs and signal functions in other species. Sexual differences in cere length, eye ring hue, rosette hue, and leg hue, and also in correlation between leg and bill hue, support the idea that the ornaments function as signals across narrow levels. Social costs of display at the colony might favour the concealment of ornament differences among individuals, necessitating close inspection of trait variation by receivers. Assessment of social consequences associated with display behaviour variation would help to clarify this issue. The observed sexual differences in ornament magnitude may reflect sex-specific breeding roles or costs of ornament production. A deeper understanding of ornament costs will require information on the genetic and physiological control of display traits. Further field efforts during seasons where breeding success is high, will inform us of associations between ornamentation, display behaviour, and breeding success.

Table 2.1 Correlations of corrected hue values sampled from two separate photos from each individual. All relationships were significant, indicating the hue sampling method was accurate.

TRAIT		r^2	F, df, p	n
Bill plates:	posterior	0.809	118.8, 64, <0.0001	67
	middle	0.709	63.8, 64, <0.0001	67
	anterior	0.718	59.4, 57, <0.0001	67
	bottom	0.758	85.3, 64, <0.0001	66
Cere		0.876	207.3, 64, <0.0001	66
Tuft		0.324	7.1, 62, <0.01	66
Ring		0.715	65.9, 64, <0.0001	66
Rosette		0.552	27.7, 64, <0.0001	66

Table 2.2. Trait length magnitude and variation for a) Females and males. of ornament lengths and non-ornament lengths. Only male ornament lengths showed greater variation than non-ornament lengths (Chi square tests). Males possess larger non-ornamental traits than females (student's t-tests). Only absolute bill depth is larger in males at the Bonferroni adjusted α (0.017) for 3 length comparisons. Body size-corrected means are least squared means from a general linear model that standardizes body size across individuals. b) Sexes pooled. Only pooled absolute ornament lengths had greater variation than non-ornamental traits.

a)

	Female			Male			Difference in means	
	Mean (mm)	CV (%)	n	Mean (mm)	CV (%)	n	t, df	p
NON-ORNAMENT LENGTH								
Tarsus	36.4	2.99	39	37.4	3.22	29	-3.546, 66	0.0007*
Culmen	206.5	2.36	40	211.5	1.75	29	-3.698, 67	0.0004*
Wing chord	58.1	3.93	40	60.1	3.24	29	-4.673, 67	<0.0001*
ORNAMENT LENGTH (Absolute)								
Tuft	105.3	7.28	38	109.2	7.14	26	-1.968, 62	0.0536
Cere	26.4	6.92	40	26.4	6.93	29	0.143, 67	0.8871
Bill depth	43.6	3.66	40	45.5	3.52	29	-4.890, 67	<0.0001*
$X^2_{0.05(1)}$, p	2.33, 0.13			3.85, 0.04				
(Body size-corrected)							F	p
Tuft	106.0	7.99	37	108.3	7.91	26	0.9944	0.3227
Cere	26.8	6.64	39	25.7	7.20	29	5.1801	0.0265
Bill depth	44.0	3.51	39	45.0	3.58	29	4.9836	0.0294
$X^2_{0.05(1)}$, p	2.33, 0.13			3.85, 0.04				

*significant at table-wide σ=0.05 using sequential Bonferroni analysis for three comparisons within each category.

b)

	Mean (mm)	CV (%)	n
NON-ORNAMENTAL LENGTH			
Tarsus	36.8	3.35	68
Culmen	208.6	2.42	69
Wing chord	58.9	3.97	69
ORNAMENTAL LENGTH			
(Absolute)			
Tuft	106.9	7.38	64
Cere	26.4	6.87	69
Bill depth	44.4	4.17	69
$X^2_{0.05(1)}$, p		3.85, 0.04	
(Body size-corrected)			
Tuft	106.8	7.26	66
Cere	26.4	6.28	67
Bill depth	44.4	3.19	67
$X^2_{0.05(1)}$, p		1.19, 0.28	

Table 2.3. Ornament hue residual magnitude and variation for a) females and males and b) all adults combined. Red skin ornaments are of greater magnitude in males. Female tuft hue is more variable in males.

a)

Trait	Female			Male			Difference in means between sexes	
	Mean	SD	n	Mean	SD	n	t, df	p
Tuft	0.13	2.64	38	-0.18	1.60	28	0.5787, 61	0.5649[†]
Cere	-1.07	4.83	38	1.46	4.39	28	-2.185, 64	0.0326
Bill	-0.04	1.57	38	0.06	1.95	28	-0.232, 64	0.8176
Ring	-0.91	1.41	38	1.23	1.11	28	-6.633, 64	<0.0001*
Rosette	-0.52	1.35	38	0.70	1.46	28	-3.499, 64	0.0009*
Leg	-0.43	1.08	38	0.60	1.08	27	-3.758, 63	0.0004*

[†] Welch's test was applied in this case due to unequal variances between sexes.

*significant at table-wide α=0.05 using sequential Bonferroni analysis for six comparisons.

b)

Trait	SD	n
Tuft	2.25	66
Cere	4.78	66
Bill	1.73	66
Ring	1.67	66
Rosette	1.52	66
Leg	1.19	65

Table 2.4. Ornament correlations of hue and absolute length for females and males. Only bill depth and cere length were significantly correlated in both sexes after Bonferroni corrections for correlations within each sex. Sample size varied from 36 to 40 (females) and 25 to 29 (males).

FEMALE	Ring	Rosette	Leg	Bill	Cere	Tuft	Tuft L.	B. Depth	Cere L.
HUE									
Ring	.	0.247	0.102	0.253	-0.151	-0.325*	-0.044	0.039	0.095
Rosette		.	0.085	0.281	0.141	-0.220	0.001	0.003	0.114
Leg			.	0.280	0.273	-0.219	-0.254	-0.240	-0.253
Bill				.	0.074	-0.209	0.020	-0.102	-0.178
Cere					.	0.296	-0.252	-0.155	-0.071
Tuft						.	0.005	0.023	-0.037
LENGTH									
Tuft							.	0.346*	0.337*
Bill depth								.	0.543***†
Cere									.
MALE	Ring	Rosette	Leg	Bill	Cere	Tuft	Tuft L.	B. Depth	Cere L.
HUE									
Ring	.	0.239	0.291	-0.037	-0.280	0.156	0.165	0.079	-0.001
Rosette		.	0.014	0.108	-0.068	0.306	0.001	0.132	0.226
Leg			.	0.579**	0.036	-0.055	-0.155	-0.089	-0.129
Bill				.	-0.002	0.189	0.106	-0.402*	-0.153
Cere					.	-0.011	0.058	-0.101	-0.058
Tuft						.	0.483*	-0.065	0.209
LENGTH									
Tuft							.	-0.031	0.121
Bill depth								.	0.803***†
Cere									.

$^{*}p < 0.05$

$^{**}p < 0.005$

$^{***}p < 0.001$

†significant at the table-wide Bonferroni adjusted $\alpha = 0.0014$ for 36 comparisons for each sex.

Table 2.5. Correlations between body condition (body size-controlled mass) and ornament magnitude. Composite statistics are for summed ranks of all ornamental traits. Negative relationships are indicated in parentheses. No results are significant at the table-wide Bonferroni adjusted alpha level of $p = 0.005$. A test of positive r-values was similarly negative for both sexes (see Results).

Trait	Pooled		Female		Male	
	r^2	n, F, p	r^2	n, F, p	r^2	n, F, p
HUE						
Ring	0.050	64, 3.29, 0.07	0.001(-)	36, 0.04, 0.83	0.002	28, 0.06, 0.81
Rosette	0.039	64, 2.49, 0.12	0.029	36, 1.03, 0.32	0.002(-)	28, 0.06, 0.82
Leg	0.016	63, 1.01, 0.32	0.003	36, 0.12, 0.73	0.020(-)	27, 0.50, 0.49
Bill	0.014(-)	64, 0.85, 0.36	0.004	36, 0.00, 0.70	0.102(-)	28, 2.97, 0.10
Cere	0.025(-)	64, 1.59, 0.21	0.028(-)	36, 0.99, 0.33	0.000	28, 0.00, 0.95
Tuft	0.002(-)	64, 0.14, 0.71	0.006	36, 0.20, 0.66	0.146(-)	28, 4.46, 0.04
LENGTH (Absolute)						
Tuft	0.001	62, 0.58, 0.45	0.019	36, 0.66, 0.42	0.009(-)	26, 0.22, 0.65
Bill depth	0.037	67, 2.47, 0.12	0.000	38, 0.03, 0.86	0.001	29, 0.03, 0.87
Cere	0.038(-)	67, 2.54, 0.12	0.017(-)	38, 0.62, 0.43	0.078(-)	29, 2.29, 0.14
Composite	0.005	58, 0.31, 0.58	0.001	34, 0.03, 0.86	0.148(-)	24, 3.82, 0.06
(Body size-controlled)						
Tuft	0.013	62, 0.77, 0.38	0.022	36, 0.76, 0.39	0.000	26, 0.01, 0.94
Bill depth	0.061	67, 4.25, 0.04	0.000	38, 0.02, 0.90	0.123	29, 3.81, 0.06
Cere	0.044(-)	67, 3.02, 0.09	0.022(-)	38, 0.82, 0.37	0.021	29, 0.58, 0.45
Composite	0.001	58, 0.33, 0.57	0.000	34, 0.02, 0.90	0.06(-)	24, 1.51, 0.23

Figure 2.1 Female and male mean ornament lengths with 95% confidence intervals for a) absolute and b) body size-controlled lengths (least square mean estimates from a general linear model). Male absolute tuft lengths were significantly greater than female absolute tuft lengths. No other differences were significantly different between sexes after Bonferroni adjustments for three comparisons each of absolute and body size-controlled length.

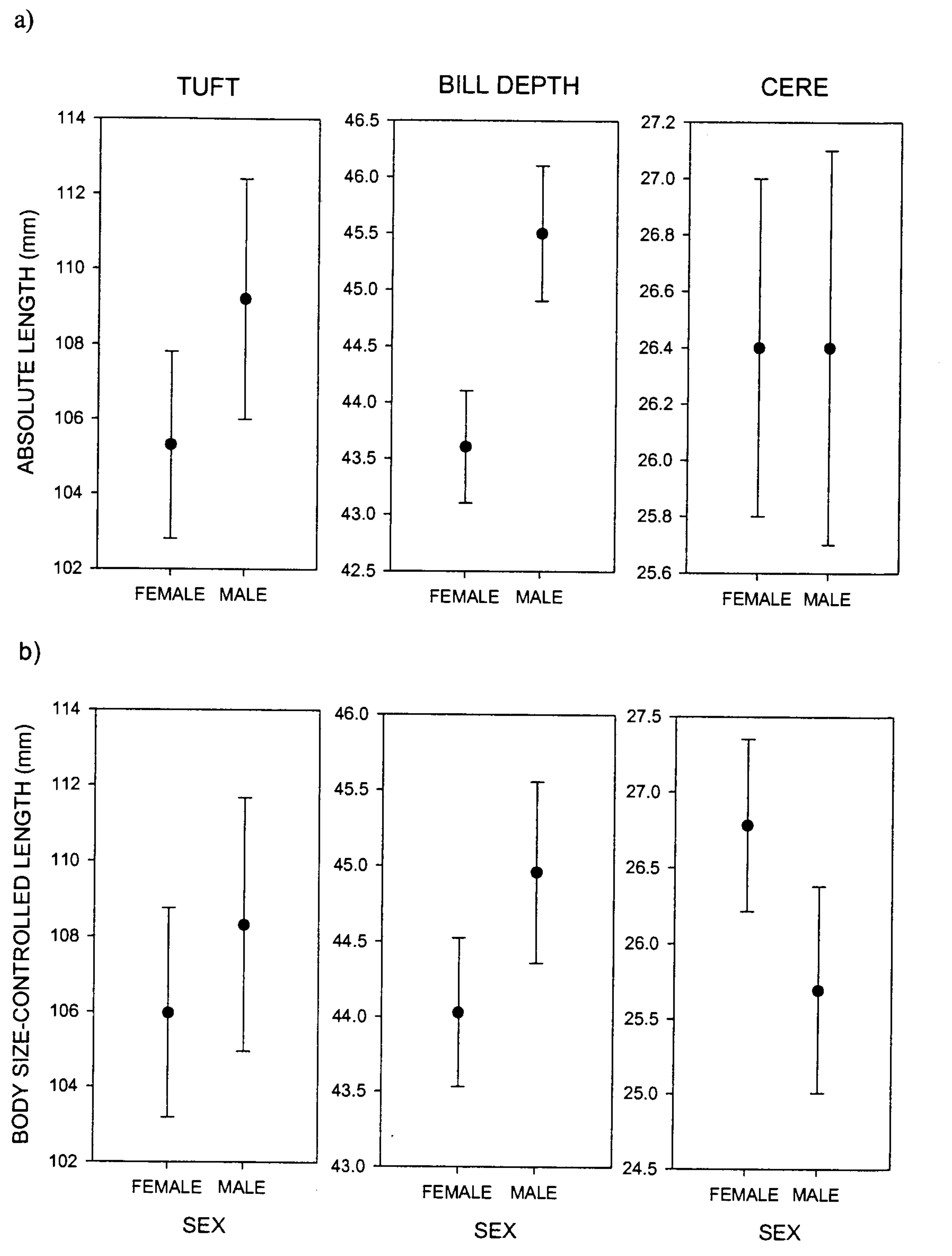
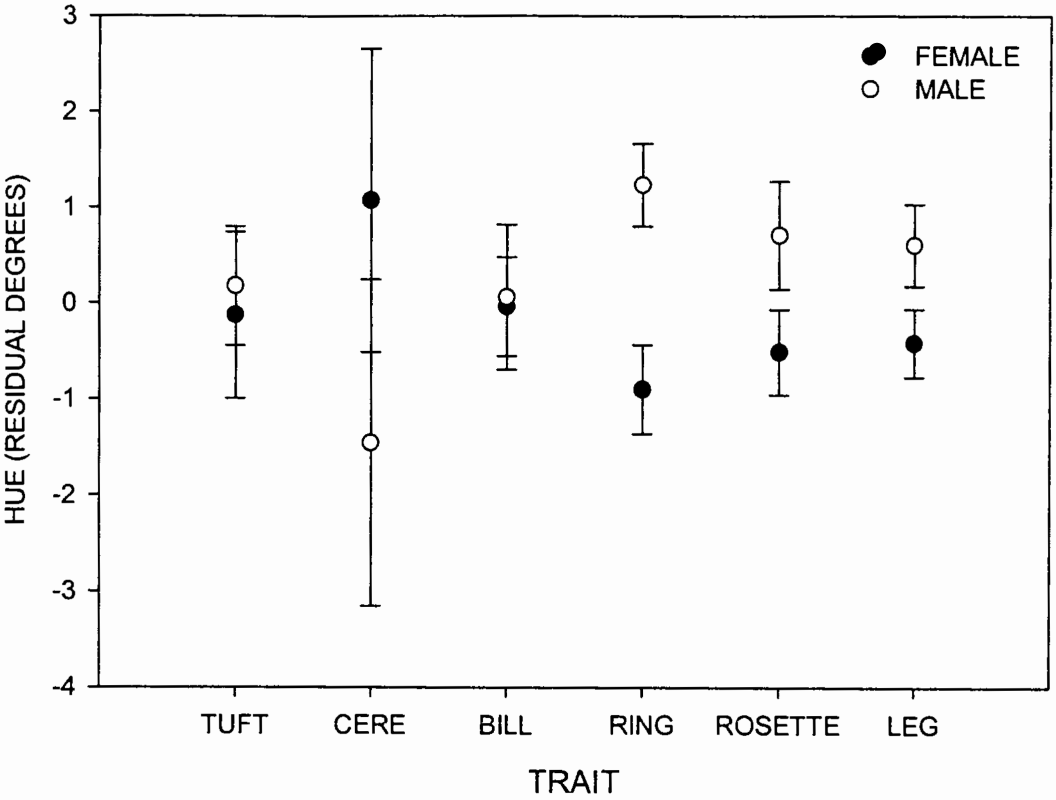


Figure 2.2 Female and male mean ornament hues with 95% confidence intervals. Males exhibited significantly redder skin ornaments (eye ring, gape rosette, and legs). No other differences were significant after Bonferroni adjustments for six hue comparisons.



3. Colony overflights by food-bearing tufted puffins in relation to kleptoparasitism by glaucous-winged gulls

Introduction

Several species of colonial alcids make patterned overflights adjacent to their breeding colonies (e.g. Taylor 1982; Gaston and Jones 1998). Variability in the occurrence and circumstances of overflight behaviour indicates that it may serve multiple purposes. Overflights appear to facilitate social activities (Gaston and Jones 1998) such as pair bonding, advertising for mates, or assessing colony-wide display levels. They may also represent searches for burrow sites by prospecting adults, or slope reconnaissance by burrow owners when there is a risk of predation or kleptoparasitism of food loads during colony attendance (Grant 1971a; Lowther et. al. 2002; Montevecchi and Stenhouse 2002). Interpretations of the function of overflights have been hindered by a lack of data on concurrent ecological conditions that may affect overflight decisions.

Overflights by tufted puffins (*Fratercula cirrhata*) on the southern side of Puffin Rock, Triangle Island (B.C., Canada), are typically in circuits of about 200-400m in diameter in front of the breeding slopes. This behaviour ranges from individual flights to the coordinated "wheeling" of hundreds of birds, and it varies in both duration and time of day. Although predation of airborne tufted puffins has not been observed at this site, adults returning to the colony with fish for their chicks risk food loss and injury during pursuit by kleptoparasitic glaucous-winged gulls (*Larus glaucescens*). Food-bearing adults at this site frequently exhibit overflight behaviour in a manner that suggests they are sensitive to gull presence and landing conditions. It is possible that overflights for these adults represent a precautionary measure against kleptoparasitism.

Several prominent ecological factors (e.g. weather, habitat grade, puffin arrival rates, gull activity) appear to be correlated with kleptoparasitism events at Triangle Island (Cassady St. Clair et. al. 2001) and other puffin colonies (Nettleship 1972; Stienen et. al. 2001). In this study, I examined whether 1) tufted puffin overflight behaviour correlates with these factors in the manner expected of evasive behaviour and (2) overflights are negatively correlated with kleptoparasitism events when these factors are statistically controlled for.

Methods

Observation protocol

Fieldwork was conducted during the tufted puffin chick-rearing period at Puffin Rock, in July and August of 2001. Two adjacent areas (approximately 10m x 20m) were marked using flags on the breeding slope. One area represented steep habitat and the second represented shallow habitat. Food-bearing puffins attempting landings in these areas were conspicuous and individually recognizable by their distinctive bill loads. Their flight paths in front of the colony could be visually tracked with binoculars from a blind located approximately 100m from the colony slope.

GSB or an assistant conducted observation shifts of 2 to 4 hours during daylight hours (05:00-22:00) on days with high slope visibility. For each adult arriving with food to a burrow within the study areas, we noted the number of overflights it made, the number of chases it received from gulls, and the outcome of the food delivery attempt. Food deliveries resulted either in successful feeds (puffins entered burrows with food loads intact) or kleptoparasitism events (puffins lost their loads following gull pursuits). Approaches were scored in categories of "0", "1 to 4", or "≥5" overflights, in order to ensure accuracy of the number of approaches by each puffin during periods of even the most frequent puffin arrivals. All data were grouped into 15-minute observation periods.

Kleptoparasitism risk appeared to be affected primarily by gulls in the immediate vicinity of the puffin breeding slope despite the consistent presence of hundreds of gulls on nearby slopes (GSB, pers. obs.). We therefore counted gulls patrolling the air space over the study area or on the ground within our study area perimeter at the beginning of each observation period. This count provided an estimate of kleptoparasitism risk across the entire study area for each observation period.

Wind direction and speed near the colony seemed to influence aerial maneuverability for both puffins and gulls. Estimates for regional wind conditions are collected each hour of the day by an automated weather station located 14 km east of Triangle Island. These data were accessed following the breeding season in the climate archives of Environment Canada (www.climate.weatheroffice.ec.gc.ca). In order to compare regional wind conditions with conditions in the immediate vicinity of the study area, we visually scored wind variables at the study area for a portion of the observation periods. Wind strength (zero, light, moderate, strong) was sampled in this case by visually estimating wind on the slope. Wind direction (northerly, southerly) was estimated by comparing wind direction on the slope and on the sea surface in front of the colony with a compass bearing.

Since all birds within this study were unmarked, the data reflect repeated observations over unknown time periods of an unknown sample of gulls and puffins. Several observations suggest that the data reflect temporally independent behavioural responses from a large sample of puffins to kleptoparasitic behaviour of several different gulls. For 11 marked burrows in which repeated puffin visits occurred within a single 4-hour observation shift, mean burrow re-visitation time was 98 ± 21(SD) minutes. Assuming roughly similar parental contributions to food provisioning (Creelman and Storey 1991), this indicates that burrow visits by individual pair members were separated on average by more than 2.5 hours ([(98 minute delivery period)-(21 minutes SD)] X [2 delivery periods per individual pair member]). Consequently, it is unlikely that colony approach behaviour by puffins or pursuit behaviour by gulls were auto-correlated via recognition between gulls and puffins or identical ecological conditions between visits. In periodic burrow surveys within the "shallow" study area, 16 burrows were confirmed to have chicks throughout most of the study period, indicating that at least 32 adults were making food deliveries within the shallow area. The "steep" study area contained a greater number of burrows, including many that were inaccessible for surveying. Based on the maximum number of puffins delivering food within a single 15-minute observation period (44), I estimate there were between 30 to 80 adults delivering food to the steep area. Numbers of patrolling gulls ranged from 1 to 20 per 15-minute observation period, but I could not keep track of which of these pursued puffins. Occasional pursuits by juvenile gulls, a leg-banded adult gull, and one footless adult gull suggest at least several gulls exhibited kleptoparasitic behaviour.

Statistics

I used the logistic regression model in Jmp 4.04 (SAS Institute) to examine factors affecting the occurrence of overflights and kleptoparasitism events. The platform uses a maximum likelihood fitting principle to fit the probability of one level of the response variable to a logistic cumulative distribution applied to a log-linear model of the independent variables. In the overflight model, I explored the affect of six variables: slope grade; and within-period estimates of food-bearing-puffin arrivals, gull presence, gull pursuit rate (gull pursuits per puffin arrival), and regional wind speed and direction. Previous work at Puffin Rock revealed that decreased slope grade correlated with a significant increase in the number of kleptoparasitism events experienced by incoming puffins, probably due to the relative difficulty experienced by puffins accessing their burrows quickly in this habitat (Cassady St. Clair et. al. 2001). Consequently, I predicted that if overflight behaviour were employed to diminish kleptoparasitism risk, it would decrease in steep habitat relative to shallow habitat. I predicted that overflights would decrease with increased puffin arrivals because kleptoparasitism risk per individual has been observed to decrease with increasing Atlantic puffin (*Fratercula arctica*) arrivals at other sites (Rice 1987). Puffins appeared to land with relatively greater control when wind blew down rather than toward the slope face, while gulls apparently hovered in with relative difficulty during downslope wind. Both gulls and puffins apparently maneuvered poorly in relatively strong wind. Consequently, I predicted that overflights would decrease when wind was downslope and increase with wind speed. Gull presence was included as an index of kleptoparasitism risk. I predicted that if puffins judge kleptoparasitism risk by assessing the number of gulls on or over the breeding slope, gull presence would be correlated with increased overflights. I also included gull pursuit rate as an index of kleptoparasitism risk, predicting that it would correlate positively with overflights if puffins incorporate both gull presence and activity to judge kleptoparasitism risk.

I predicted that overflight behaviour would negatively correlate with kleptoparasitism events when the other ecological variables were controlled for in the kleptoparasitism model, due to its hypothesized compensatory effect under conditions of increased kleptoparasitism risk. I made no prediction about the direction of the relationship between kleptoparasitism events and wind speed, because I was not sure how it affects the relative flight abilities of gulls versus puffins. Predictions for the remaining variables were the same as for the first model. I made no prediction about the strength of any relationships because of the hypothesized compensatory effect of overflight behaviour.

Results

We observed 3272 individual food delivery attempts during 144.25 observation hours conducted between July 7 and August 23, 2001. Table 3.1 summarizes raw proportions of food deliveries and kleptoparasitism events among the three overflight categories. Overflights typically ranged between 1 and 4 and were involved in nearly 11% of the total food delivery attempts across the entire study area. The proportion of kleptoparasitism events experienced by individuals increased with the number of overflights made when considered across the entire study area (Pearson Chi-square: $X^2 = 106.7$, $DF = 2$, $P < 0.0001$) and also the steep ($X^2 = 50.66$, $DF = 2$, $P < 0.0001$) and shallow ($X^2 = 44.13$, DF = 2, $P < 0.0001$) grades separately. The slight decrease in proportion of kleptoparasitism events experienced by puffins making 5 or more overflights compared to 1 to 4 overflights on the steep habitat was not statistically significant ($X^2 = 1.26$, DF = 1, P = 0.262). These results indicate that, if overflights are implemented to reduce kleptoparasitism when the risk is high, they are not perfectly effective at this task. However, an ecological context for the occurrence of individual overflights is required to more clearly evaluate the role of this behaviour in kleptoparasitism.

Overflight model

The first logistic model explores whether overflight behaviour was related to ecological and physical factors expected to influence kleptoparasitism risk. Results from this model are reported in Table 3.2. Parameter estimates refer to the change in the odds of "0" versus "1 to 4", "0" versus "≥5", and "1 to 4" versus "≥5" overflights, respectively, for a one-unit change in each of the independent variables (Table 3.2a). Parenthetical values refer to the percentage change in the odds for a one-unit change in each of the independent variables (or for a change to the category indicated for categorical data). For the continuous variables, the model calculates the parameter estimates from a linear model for each variable found by least squares. For the categorical grade variable, the model calculates the parameter estimates as the difference from the average response value across both levels. Chi-square and probability values are for negative likelihood ratio tests of overall factor effects (Table 3.2b).

The whole model significantly improved the fit to the data compared to a reduced model that contained only the intercepts for "1 to 4" and "≥5" overflight categories (X^2 = 314.97, DF = 12, $P < 0.0001$). Due to the categorical nature of the response data, I could not establish a reliable estimate of total variation in the data explained by the model. All variables significantly contributed to the overflight model and in the direction predicted for anti-kleptoparasitism behaviour. Overflight behaviour correlated negatively with steep slope grade, compared to shallow slope grade. This result supports the idea that overflights are used more in shallow habitat where kleptoparasitism risk is relatively greater than on steep habitat. Overflights also correlated negatively with puffin arrivals, as expected if increased arrivals compensate for kleptoparasitism risk and diminish the need for overflight behaviour. Regional wind direction ranged from 1 to 36°. Increased regional wind direction was correlated with a transition from upslope to downslope wind direction at the study area (logistic regression: $X^2 = 94.64$, $p < 0.0001$). Overflights decreased as regional wind direction increased (i.e. during downslope winds). Conversely, overflights were positively correlated with factors expected to increase kleptoparasitism risk. Overflights increased with gull presence and pursuit rate of gulls, suggesting that if incoming puffins adjust their behaviour to compensate for perceived kleptoparasitism risk, gull activity levels and numbers on or over the slope may represent a reliable cue. Regional wind speed ranged from 36 to 70 km/h. Regional wind speed was positively correlated with wind speed in the vicinity of the study area (logistic regression: $X^2 = 181.65$, $p < 0.0001$). The likelihood of overflights occurring increased as regional wind speed increased, but there was no change in the category of overflights with increasing wind speed.

The results of the overflight model suggest potential direct relationships between several physical and ecological variables of presumed importance to kleptoparasitism risk, and the number of overflights made by food-bearing puffins. In order to examine the relative importance of these variables, I created a second logistic model with overflights and the six independent variables from the first model as regressors.

Kleptoparasitism model

Results from the kleptoparasitism model are reported in Table 3.3. Coefficient estimates refer to the odds of the first response level (i.e. zero kleptoparasitism, or the probability of a successful food delivery) with respect to each of the independent variables. The whole model significantly improved the fit to the data over the reduced model ($X^2 = 136.04$, DF = 8, $P < 0.0001$). Several variables correlated with kleptoparasitism events independently of the effect of other factors. Surprisingly, overflights strongly correlated with kleptoparasitism events in the opposite direction to my prediction. This result was driven by a strong negative change between deliveries in the "0" versus "1 to 4" overflight category from the average for zero kleptoparasitism events. The "≥5" category showed a smaller but also negative change compared to the "0" overflight category. This result presents evidence against the role of overflights as an effective anti-kleptoparasitic tactic. Kleptoparasitism events decreased with increased slope grade, supporting previous results (Cassady St. Clair et. al. 2001), and also decreased with increased puffin arrivals. Kleptoparasitism events decreased with increasing regional wind direction, in support of my observation that kleptoparasitic food-bearing puffins appear to generally have a aerial advantage over gulls in conditions of downslope winds. Kleptoparasitism events increased with pursuit rate as I predicted, but was unrelated to the number of gulls present. Wind speed was not correlated with kleptoparasitism events, suggesting that neither species has a strong advantage across the range of documented wind speeds.

Discussion

My results provide mixed support for the function of puffin overflights as an anti-kleptoparasitism strategy. Overflights generally appeared to help food-bearing puffins to avoid landing near gulls, to evade close pursuit during landing attempts, and to make accurate landings. Further, all ecological factors that I examined contributed significantly to the overflight model in directions that support the role of overflights in reducing kleptoparasitism; overflights correlated positively with gull presence, gull pursuit intensity, wind speed, and upslope winds, and correlated negatively with slope grade, and numbers of puffins arriving at the colony. However, in a second model that controlled for these factors, overflights were positively correlated with kleptoparasitism events. Below, I review these results and discuss the possibility that unmeasured variables or a different function of overflights account for the conflicting results.

It is possible that multiple overflights diminish kleptoparasitism success on steep terrain, although too few kleptoparasitism events occurred on the steep plot to separately examine these data with respect to ecological variables. The utility to food-bearing puffins of performing multiple overflights is probably governed by overflight costs to puffins relative to vigilance costs to gulls (Brockman and Barnard 1979; Rice 1987). Multiple overflights at my study site were rare (only a few instances were observed of more than about 10 overflights), suggesting that if sustained overflight behaviour is beneficial, it typically offers rapidly diminishing returns to puffins.

Despite the increased kleptoparasitism events associated with overflight behaviour, overflights were correlated with several ecological factors in precisely the manner expected of evasive behaviour. First, overflight behaviour was negatively correlated with the rate of puffin arrivals and positively correlated with gull presence and pursuit rate (Table 3.2), suggesting it can help counteract increased kleptoparasitism risk associated with low puffin arrival rates or high gull activity. Victim group size influences pursuer success (e.g. Landeau and Terborgh 1986; Uetz and Hieber 1994; Burger and Gochfeld 2001) or victim evasive behaviour (e.g. Boland 2003; Fernandez et. al. 2003) in various systems. Victims in groups benefit from pursuer confusion (Landeau and Terborgh 1986; Litvak 1993; Schradin 2000) and decreased individual chances of being captured (Burger and Gochfeld 2001). The negative relationship between kleptoparasitism events and puffin arrivals (Table 3.3) may reflect greater difficulty for gulls to isolate target puffins as puffin numbers increase, or interference competition among gulls (Pierotti 1983; GSB, pers. obs.). Clustered arrivals of food-bearing Atlantic puffins over several seconds (Merkel et. al. 1998) have been argued to swamp kleptoparasitic gulls (Grant 1971; Ashcroft 1976), and Pierotti (1983) presented anecdotal support for the idea that overflights may help Atlantic puffins coordinate clustered landings. Clusters generated by overflights could explain the decrease in overflights during increased total puffin arrivals and the increase during high gull presence or activity, if the need for puffins to coordinate landings varies according to the ratio of puffins to gulls. Observations of individual landing times and locations will be required to clarify the temporal and spatial distributions of tufted puffin arrivals at Puffin Rock, and the role that overflights might play in structuring these distributions.

Second, the occurrence of 5 or more overflights was associated with north and strong regional winds (correlating at the study site with upslope and strong winds, respectively)(Table 3.2). High wind speed and winds blowing upslope appeared to diminish both the control and accuracy with which puffins landed on the colony. In upslope wind conditions, many landings resulted in birds either missing their burrows by up to several meters or tumbling to the ground and then having to scramble toward their entrances. Other birds achieved a controlled landing by using a slow approach and employing much flapping immediately prior to touching the ground. In either case, landing efficiency was apparently reduced. Conversely, gulls appeared to maneuver easily during upslope drafts relative to during calm conditions or downslope winds. Hence, the wind data are consistent with the idea the overflights help to compensate for the decreased flight control and potential kleptoparasitism risks associated with upslope and strong winds.

Finally, if overflights help adults to assess current landing conditions and the precise location of their burrow, then the challenges of landing on shallow terrain may explain the significant negative correlation between slope grade and overflight behaviour (Table 3.2). Puffins landing on shallow terrain apparently required a shallower flight trajectory and slower approach, relative to puffins landing on steep terrain. They occasionally missed their burrows by up to several meters upon landing, and then either scrambled around in the grass searching for their entrance or took to the air for a second landing attempt. Take-offs were never made from within the shallow terrain, even during close pursuit or contact by gulls; instead, individuals walked or scrambled by foot out of the shallow area and flew from the upper lip of steeper terrain. A more detailed analysis of slope features and occurrence of kleptoparasitism at this site arrived at a similar negative correlation between slope grade and kleptoparasitism events (Cassady St. Clair et. al. 2001).

Interactions between puffin overflights and gull pursuits during the course of individual food delivery attempts may restrict the potential evasive function of overflight behaviour. Gull behaviour indicated that overflights might notify gulls of the likelihood and slope location of impending delivery attempts (Pierotti 1983). Consequently, overflights may seldom compensate through improved landing efficiency for the increased gull attention that they provoke, particularly when they are made following failed landings or close encounters with gulls. In this respect, overflights may often occur as an emergency measure, used only when immediate kleptoparasitism risk (i.e. upon closely approaching the burrow) is high. A thorough evaluation of the role of overflights in kleptoparasite evasion may therefore require consideration of the precise circumstances under which overflights are initiated, including occurrence of gull encounters and aborted landing attempts during the first aerial pass, as well as estimation of the intensity of gull pursuits for individual food delivery attempts. In addition, quantification of landing efficiency while controlling for interacting variables will help to clarify the relationship between overflights and landing efficiency.

Individual differences such as flying ability, physical condition, or breeding status may affect the frequency and success of overflight behaviour, and may represent critical variables missing from the current analysis. In a study of Atlantic puffins (*Fratercula* *arctica*) in Newfoundland, Nettleship (1972) noted greater body size and mass among adults nesting in relatively steep habitat, and increased kleptoparasitism rates in relatively shallow habitat. My data indicate that overflights were proportionately more common among puffins landing on shallow versus steep habitat (Table 3.2). This study may have controlled for individual differences correlated with habitat grade. Observations of marked individuals of known condition, breeding status, and parental quality may identify subsets of the population that differ in kleptoparasitism risk or the utility of overflights in mitigating this risk.

Display or other social behaviour represents an alternative explanation for the occurrence of apparently costly overflights. Food displays occur among several seabird species, including murres (GSB, pers. obs.; Gaston and Jones 1998). At my study site, I observed paired overflights by courting puffins, and overflights by many unmarked adults that may have been using this behaviour to display or inspect other birds. Food-bearing puffins were not observed when courting is most intense prior to the nestling period, and no stylized food display was observed on the slopes by individuals or among pair members. To the contrary, individuals arriving with food appeared intent on entering their burrow and usually did so within several seconds of landing. Those who misplaced their burrow either scrambled to find it or discreetly searched the immediate vicinity. Diminished overflights during high puffin arrival rates are also unsupportive of a display function of overflights in food-bearing puffins. Finally, the significant relationships that I observed between overflights and wind conditions, slope grade, and gull activity, further suggest response by food-bearing puffins to adverse landing conditions rather than display or inspection opportunities, since there is no compelling social motive for these patterns. To the extent that food display or general social behaviour may occur among food-bearing adults, it would probably be associated with individuals lacking or changing mates. Observations of marked birds of known breeding status would be required to examine this possibility.

The purpose and benefit of puffin overflight behaviour to avoid capture seems clear at colonies where gulls prey on adult puffins (Harris 1980; Pierotti 1982; Taylor 1982), and is supported by my observations of individual interactions between puffins and kleptoparasitic gulls on Triangle Island, and the correlations between overflights and ecological variables that may affect landing conditions at this site. If puffin overflights generally have an evasive motive, then the energy costs associated with this or other compensatory behaviour may have a significant negative impact on colony-wide reproductive success that does not translate into within-season differences in reproductive success across adjacent habitats or individuals. Hence, the reported minimal affect of kleptoparasitism on tufted puffin breeding success at Triangle Island (Cassady St. Clair et. al. 2001) and on alcids at other colonies (Pierotti 1983; Wilson 1993) may partially reflect varying degrees of compensatory behaviour by food-bearing adults to varying degrees of kleptoparasitism risk. Data from other puffin colonies that contain nesting areas with and without gulls (i.e. highly contrasting predator regimes) support the idea that kleptoparasitism can affect breeding prospects (Nettleship 1972; Finney et. al. 2003; GSB, unpublished data). Further support for this idea would come from observations of higher nest abandonement rates in habitats relatively vulnerable to kleptoparasitses, or longterm reproductive declines in areas where kleptoparasitism persists. At Triangle Island, consistently greater prey size observed in an area of the colony with few gulls also raises the possibility that kleptoparasitism risk affects prey selection (GSB, unpublished data).

Conclusions

Clarifying the role of overflight behaviour in mediating interactions with kleptoparasites or predators will likely entail further studies that examine overflight behaviour while simultaneously controlling for correlated ecological variables. My efforts in this direction point to several considerations for future work at Puffin Rock. First, behaviour in the current study may have been sampled at too large a scale to detect details determining overflight success. Since puffin and gull intentions may interact during the course of individual food delivery attempts, further efforts should consider the detailed circumstances of colony approach and overflight initiation, and also the intensity of gull pursuits, in order to decipher the relationship between these behaviours. This approach might distinguish between levels of kleptoparasitism risk that my protocol missed. Second, individual differences in flight ability or ecological context might represent a key variable that is absent in the current analysis. Observations of overflight behaviour by marked individuals of known condition and breeding status are likely to provide critical insight to the utility of overflights to kleptoparasitism evasion in this respect. Third, if overflights generally put puffins at greater risk of kleptoparasitism, then other potential benefits to puffins of this behaviour deserve attention. If there is a social component to overflights, observations of marked individuals should reveal biases of this behaviour toward individuals benefiting most from this function, such as unmated individuals or failed breeders.

Table 3.1 Summary of approaches by food-bearing puffins and kleptoparasitism events for the different overflight categories. The parenthetical value beside each total kleptoparasitism value is the percentage of total approaches for that habitat category resulting in kleptoparasitism events. All other parenthetical values are the percentage of the total within each column.

Overflight category	Shallow		Steep		Entire study area	
	Approaches (% total)	Kleps. (% total)*	Approaches (% total)	Kleps. (% total)*	Approaches (% total)	Kleps. (% total)*
0	629 (84.3)	8 (34.8)	2291 (90.7)	5 (38.5)	2920 (89.2)	13 (36.1)
1 to 4	93 (12.5)	11 (47.8)	203 (8.0)	8 (61.5)	296 (9.0)	19 (52.8)
≥5	24 (3.2)	4 (17.4)	32 (1.3)	0 (0.0)	56 (1.7)	4 (11.1)
Total	746	23 (3.1)	2526	13 (0.5)	3272	36 (1.1)

*significantly higherproportions of kleptoparasitism events experienced by individuals making overflights ($p < 0.0001$).

Table 3.2 Ecological and physical factors affecting overflight behaviour, showing a) odds ratio parameter estimates for each level of the variables. Parenthetical values indicate the percentage change in the odds of overflights occurring for a one-unit change in the odds ratio of the independent variable. b) negative likelihood ratio tests of the overall contribution of individual variables to the model.

a)

Variable		Parameter estimates		
		“0” versus “1 to 4"	“0” versus “≥5”	“1 to 4” versus “≥5”
Steep	(vs. shallow)	1.45 (45)	2.13 (113)	1.47 (47)
Puffin arrivals	(#/15min)	1.05 (5)	1.12 (12)	1.06 (6)
Wind direction	(degrees)	1.05 (5)	1.07 (7)	1.02 (2)
Gulls present	(#/15min)	0.98 (-2)	0.86 (-14)	0.88 (-12)
Pursuit rate	(#/approach)	0.38 (-62)	0.22 (-78)	0.58 (-42)
Wind speed	(km/h)	0.99 (-1)	0.99 (-1)	1.00 (0)

b)

Variable	DF	Chi square	P
Slope grade	2	11.62	0.003
Puffin arrivals	2	73.97	<0.001
Wind direction	2	45.92	<0.001
Gulls present	2	7.28	0.026
Pursuit rate	2	41.15	<0.001
Wind speed	2	10.03	0.007

Table 3.3 Ecological and physical factors affecting kleptoparasitism events, showing a) odds ratio parameter estimates for each level of the variables. Parenthetical values indicate the percentage change in the odds of kleptoparasitism occurring for a one-unit change in the odds ratio of the independent variable. b) negative likelihood ratio tests of the overall contribution of individual variables to the model.

a)

Variable		Parameter estimate
Overflights	(vs. 0)	
	1 to 4	0.20 (-80)
	≥5	0.71 (-29)
Slope grade	(vs. shallow)	
	steep	1.45 (45)
Puffin arrivals	(#/15min)	1.06 (6)
Wind direction	(degrees)	1.12 (12)
Gulls present	(#/15min)	0.95 (-5)
Pursuit rate	(#/approach)	0.37 (-63)
Wind speed	(km/h)	0.98 (-2)

b)

Variable	DF	Chi-square	P
Overflights	2	16.24	<0.001
Slope grade	1	15.05	<0.001
Puffin arrivals	1	4.42	0.035
Wind Direction	1	20.21	<0.001
Gulls present	1	0.45	0.501
Pursuit rate	1	10.20	0.001
Wind Speed	1	1.93	0.164

4. General Conclusions and Research Suggestions

Sexually selected traits are traditionally considered to be extravagant and limited by selection for traits more directly linked to survival or reproduction. Yet tufted puffins provide an extreme example of morphological breeding display compared to most other seabirds, while breeding under apparently severe ecological constraints (e.g. long nestling period despite biparental care of a single nestling, narrow nestling diet, distant foraging grounds, high adult wingload, apparently variable prey resources). Clearly, many of the constraints that we typically consider limiting to the breeding effort are not currently prohibiting display in this species. Either the evolution of display traits under ecological constraints is more flexible than we normally appreciate, or the ornaments currently possessed by tufted puffins evolved under a different ecological scenario from the present. The former of these two ideas suggests that other ecological factors such as high adult survival rates and display in large groups might strongly favour the evolution of ornaments. The latter suggests that extravagant display may be maintained even under severe current ecological constraints, and raises the intriguing possibility that display traits may restrict the rate or scope of ecological adaptation in response to viability selection. It is possible that elements of both ideas are true. Colony-wide breeding success is quite variable across years at Triangle Island and other puffin colonies with longterm data, relative to breeding success of other colonial seabirds. Environmental stochasticity (e.g. prey density fluctuations, competition, predation or kleptoparasitism risk) probably plays a prominent role in this variation. If tufted puffins require consistently favourable conditions to raise nestlings to fledgling condition, but have no guarantee that favourable conditions will persist, then selection might favour long-lived adults that on average invest only modest effort in current parenting (i.e. during either favourable or poor breeding conditions). This situation might in turn leave breeding adults with resources and time to respond relatively strongly to selection for breeding display. In a colonial system where breeding burrows are limited and mate quality is critical to breeding success, this selection might be relatively strong, such that parental effort decisions would be heavily discounted by display opportunities for better burrows or mates. Under this scenario, breeding adults would be selected to bear extravagant ornaments despite apparently adverse breeding conditions. The stochastic environment could maintain an evolutionary focus on display and limit the ability of tufted puffins to respond to viability selection during periodic or permanent resource changes (e.g. to invest high parental effort during favourable conditions, to pursue alternative prey choices during poor conditions, or to respond to gradual shifts in prey communities). The same scenario might also develop from initially different ecological conditions that also foster the evolution of extravagant ornaments, such as predictable and favourable environmental conditions.

The complexity and ecological circumstances of tufted puffin breeding ornaments suggest that research on this system will provide unique insights to the evolution of signaling strategies and display traits. My initial efforts in this direction reveal a few interesting patterns. Given the variety of materials and structures comprising their many breeding ornaments, it might be expected that tufted puffin ornaments transmit information between intra-specific competitors or prospective mates. Yet the ornaments measured in the present study exhibited only slight variation in hue and length among individuals. The primary cost of ornamentation in this species might occur during aggressive interactions over mates or breeding burrows, favouring general concealment of individual status. In light of this pressure, prolonged mating rituals and interactions with neighbours on the colony may allow tufted puffins to decipher differences among traits on the fine scale that I observed. If this interpretation is correct, then my results suggest that breeding displays can function as signals across narrower ranges than are typically acknowledged. This idea is currently supported by the slight male-biased sexual dimorphism I documented in skin hues. Alternatively, ornaments may only enhance mating displays for which behavioural aspects provide critical variation. Comparison of ornamental and behavioural variation with respect to the outcome of mate competition and choice will contribute a useful step toward separating these signalling possibilities. Observations of the performance and breeding success of marked puffins during seasons with relatively high fledge rates will provide insight to other fitness correlates of these traits. The lack of pairwise or collective correlation observed among the traits in the present study suggests that such fitness correlates may be diverse, as is apparent in other taxa.

If puffins use colony overflights to evade kleptoparasitism or predation, the energetic costs associated with this and other compensatory behaviours may have a significant negative impact on their reproductive efforts that is not immediately apparent across different habitats under similar predator regimes. This idea is supported at other seabird colonies that contain areas with and without kleptoparasites or predators, in which puffins experience greater reproductive success in the latter areas. The costs of kleptoparasite evasion may partially determine colony success or failure during seasons of marginal breeding conditions that frequently occur at Puffin Rock. This highlights the need to understand the role of behavioural tactics in mediating interactions between puffins and gulls. The purpose of colony overflights is difficult to isolate because various ecological factors may simultaneously affect kleptoparasitism risk or the efficacy of overflight behaviour. In the present study, I focussed on the relationship between overflights of food-bearing puffins and kleptoparasitism events by glaucous-winged gulls while statistically controlling for other ecological factors. Overflights were correlated with each factor in a manner predicted of evasive behaviour; they were positively correlated with gull presence, gull pursuit intensity, and wind speed, and negatively correlated with habitat grade, puffin arrival rates, and downslope wind direction. However, controlling for these variables revealed a positive correlation between puffin overflights and kleptoparasitism events. This result suggests that, during the current season of study, overflights did not help to diminish kleptopoarasitism risk and may have contributed to kleptoparasitism events. Future efforts might focus on the interaction between individual puffin overflights and gull pursuits to better understand when, if ever, overflights help puffins to avoid gulls. Information is also needed about whether landing efficiency is improved by overflights. The greatest contribution might be made by observations of marked puffins, particularly those of known age and breeding status. Such observations will quickly identify whether overflight behaviour is limited to a subset of the population such as those changing mates, or inexperienced or otherwise poor quality parents.

Research on the relationship between kleptoparasitism risk and tufted puffin prey selection might provide additional insight to the effects of kleptoparasitism on tufted puffin evasive tactics and breeding prospects. If provisioning success is partially determined by the likelihood of detection or capture by kleptoparasites upon colony approach, then kleptoparasitism risk might affect tufted puffin decisions regarding the size, shape, or quality of their prey. This consideration further suggests that puffin prey returns to the colony may not only reflect prey availability at puffin foraging grounds, but also a direct interaction between gull and puffin foraging decisions. Future efforts to investigate this possibility might focus on prey returns in light of interactions between puffins and gulls at closely situated but distinct puffin breeding slopes with highly contrasting kleptoparasite densities, such as those occuring at Triangle Island.

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