Relationships between mercury burden, sex, and sexually selected feather ornaments in Crested Auklet (*Aethia cristatella*)

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Abstract

Individuals with higher contaminant burdens are expected to be in poorer physical health and be of lower individual body condition and energetic status, potentially resulting in reduced ornamentation or increased asymmetry in bilateral features. The degree and magnitude of this effect also would be expected to vary by sex, as female birds depurate contaminants into eggs. We tested for relationships among mercury in feathers, sex, and elaborate feather ornaments that relate to individual quality in Crested Auklets (*Aethia cristatella*), small planktivorous seabirds in the North Pacific Ocean. We found no relationships between mercury and the size of individuals' forehead crest, or degree of measurement asymmetry in auricular plumes, both of which are favoured by intersexual selection. Females had significantly greater mercury concentrations than males (females: 1.02 ± 0.39 µg/g, males: 0.75 ± 0.32 µg/g); but concentrations were below that known to have physiological effects, as expected for a secondary consumer. Sex differences in overwintering area for this long-distance migrant species (more females in the Kuroshio Current Large Marine Ecosystem than males) could be the reason for this seemingly counterintuitive result between sexes. Further research relating mercury burden to overwintering ecology and diet contents would build on our results and further elucidate interrelationships between sex, sexually selected feather ornaments and contaminant burden.

Key words: Alcidae; asymmetry; mercury; ornament; quality.

Introduction

Mercury (Hg) is a pervasive global contaminant that is largely produced anthropogenically, and projected to increase into the future (Driscoll et al. 2013; Krabbenhoft and Sunderland 2013; Lamborg et al. 2014; Lindberg et al. 2007; Selin 2014; Streets et al. 2009). As a potent neurotoxin, it can have detrimental effects on wildlife, including changes in physiology, behaviour, and survival (Ackerman et al. 2016b; Goutte et al. 2014; Heinz et al. 2009; Jackson et al. 2016; Thompson 1996; Weiner et al. 2003). Understanding which species are at risk from high concentrations of contaminants such as Hg, and what factors influence those conditions is therefore an important goal for managers and conservation biologists (Golden and Rattner 2003; Provencher et al. 2014; Thompson 1996). Mercury contamination in oceans and its prevalence in marine food chains is related to atmospheric fallout of particulates originating mostly from Asian coal burning (Pacyna et al. 2006) and its subsequent transformation into toxic methyl mercury (MeHg) (Sunderland et al. 2009).

Birds are effective monitors of Hg in the environment, because they can integrate signals over space and time, Hg in tissues is dietary in origin, and tissues can easily be sampled non-destructively (Monteiro and Furness 1995; Monteiro and Furness 2001; Monteiro et al. 1998). Birds regulate their Hg body burden by excreting the toxic form of Hg, MeHg into growing feathers (Bond and Diamond 2009), which are inert once fully grown. The Hg in feathers is bound to disulphide bonds, and remains stable (Appelquist et al. 1984; Crewther et al. 1965), allowing for a retrospective examination of Hg exposure (Bond et al. 2015; Vo et al. 2011).

A variety of factors affect Hg concentrations in birds, including proximity to point sources (Finger et al. 2015; Jackson et al. 2011), trophic position and diet (Becker et al. 2002; Elliott and Elliott 2016), age class (Thompson et al. 1991), and sex (Robinson et al. 2012). Individuals closer to Hg sources, those at higher trophic positions, and adults tend to have higher Hg than individuals farther from sources, at lower trophic positions, and chicks. Males are generally thought to have higher Hg concentrations than females, as females can also eliminate Hg in eggs (Braune and Gaskin 1987b; Lewis et al. 1993; Monteiro and Furness 2001; Robinson et al. 2012).

Crested Auklets (*Aethia cristatella*) are small planktivorous seabirds breeding around the Bering and Okhotsk Seas, have a diet of mostly euphausiids and calanoid copepods, and lay a single egg each year (Bond et al. 2012; Jones 1993a). Crested Auklets are socially monogamous and have elaborate sexually monomorphic feather and bill ornaments that are displayed during courtship (Jones et al. 2000). Their most prominent feather ornament is a conspicuous forehead crest that experiments showed to be a product of mutual sexual selection, and paired white auricular plumes (Jones and Hunter 1993; Jones et al. 2000; Jones et al. 2004). Although Crested Auklet males have a larger body size and proportionally larger bills than females, crest and auricular plume length are sexually monomorphic (Jones 1993b; Jones et al. 2000). Like many sexually selected traits, Crested Auklet crest length and the degree of measurement asymmetry of the auricular plumes are highly variable in expression across individuals of both sexes (Jones et al. 2000). This kind of variability in a sexually selected trait has been suggested to relate to its function as an indicator of individual quality in mate choice (Van Valen 1962; Zahavi 1975), in which individuals benefit either directly or indirectly by mating with healthy individuals as indicated by the expression of the sexually selected or more symmetrical trait (Spencer and MacDougall-Shackleton 2011). Nevertheless, there are few clues as to what aspect of quality Crested Auklet crests might signal as no relationships between body condition and survival have been found (Jones et al. 2000; Jones et al. 2004). There is also the question of why variability in crest length is greater in females than in males (Jones et al. 2000).

In other taxa, greater Hg concentrations have been associated with the degree of asymmetry of feather traits, though not in all cases (Evers et al. 2008; Herring et al. 2016). Here we aimed to test for relationships of mercury burden, sex and sexually selected feather ornaments in this spectacularly ornamented sexually monomorphic seabird. We predicted that Crested Auklet males would have higher feather Hg than females because females can eliminate Hg in eggs, and that individuals with longer crests and more symmetrical auricular plumes, being in better condition, would have lower feather Hg concentrations.

Methods

We collected feather samples from Sirius Point, Kiska Island in the western Aleutian Islands, Alaska (52º 08'N, 177º 36'E) in June and July 2009 (n = 28) and 2010 (n = 6); no individuals were sampled more than once. Birds were captured on the colony surface using noose carpets (Jones et al. 2004), aged (adult or sub-adult) following Bédard and Sealy (1984), and sex determined from bill morphology (Jones 1993b). We restricted our samples to adult birds, and an equal number of females and males (n = 17 of each sex). Birds were weighed using an electronic balance (± 1 g), and we measured crest length (± 0.1 mm) and length of the auricular plumes (± 0.1 mm) using callipers (Jones et al. 2000; Jones et al. 2004). Measurement asymmetry of auricular plumes was calculated as: $\sqrt{(\text{left} - \text{right})^2}$; all measurements were performed by one individual (ALB).

Two breast feathers were plucked and placed in individual paper envelopes. Crested Auklets replace breast feathers and feather ornaments prior to breeding as in other *Aethia* spp. auklets (Bédard and Sealy 1984; Bond et al. 2013; Pitocchelli et al. 2003; Pyle 2008). Feathers therefore represent the accumulation of Hg since the previous moult, the same period over which they can invest in ornamentation.

Feathers were placed in sterile glass scintillation vials, washed in a 2:1 (v/v) chloroform/methanol solution to remove external contamination (Borghesi et al. 2016), and air dried for 24 h at ambient room temperature. We analysed two feathers from each individual (Bond and Diamond 2008) using a DMA-80 (atomic absorption spectrometry; Milestone, Ltd) (Haynes et al. 2006). Feathers were placed in nickel boats and kept in place using glass capillary tubes and Nanopure deionized water. Method blanks consisting of capillary tubes and water were all below the level of detection (0.04 ng Hg).

We analysed three certified reference materials (CRMs) for quality assurance and control: lobster hepatopancreas (TORT-3, National Research Council of Canada; certified concentration ± expanded uncertainty (U_{CRM}; Joint Committee for Guides in Metrology 2008): 0.292 ± 0.022 µg/g, recovery: 113 ± 2 %, n = 8), dogfish muscle (DORM-4, National Research Council of Canada; certified concentration: 0.412 ± 0.036 µg/g, recovery: 106 ± 1 %, n = 8), and human hair (IAEA-85, International Atomic Energy Agency; certified concentration: 23.20 ± 0.06 μg/g, recovery: 98 ± 1 %, n = 5).

Statistical methods

We assessed normality of Hg data using Shapiro-Wilk's test (Shapiro and Wilk 1965), and then constructed a series of general linear models using year of collection (2009 or 2010), and sex (male or female) as predictors. We also included crest length, and asymmetry of auricular plumes (and their interactions) to predict feather Hg, as they can also act as a signal of individual quality (Jones 1993a; Jones et al. 2000; Jones and Montgomerie 1991a; Jones and Montgomerie 1991b). Models were compared using Akaike's Information Criteria adjusted for small sample size (AIC_c) using the package *AICcmodavg* (Mazerolle 2017); models with $\Delta AIC_c > 2$ were not considered competitive. Model terms were considered significant when $p < 0.05$. We calculated the effect size using Hedge's *g* (an unbiased estimator of the standardized mean difference) (Hedges 1982) using the package *compute.es* (Del Re 2013) in R 3.3.2 (R Core Team 2018). Differences in morphometrics were assessed using t-tests. Data are presented as means ± SD.

Results

Data were normally distributed (Shapiro-Wilk's $W = 0.95$, $p = 0.09$), so Hg data were not transformed. Males had longer auricular plumes than females (males: 33.1 ± 8.1

mm, females: 27.6 ± 6.7 mm; $t_{32} = 2.17$, $p = 0.038$), but crest length did not differ between sexes (36.3 ± 5.5 mm; $t_{32} = -1.48$, $p = 0.15$). The model for predicting feather Hg that included sex received the most support ($w_i = 0.73$); no other model had $\Delta AIC_c < 2$, and models that included ornaments were not competitive ($\Delta AIC_c < 9.8$; Table 1), so results are from the top-ranked model only. Feather Hg was significantly higher in females (1.02 ± 0.39 μg/g) than in males (0.75 ± 0.32 μg/g; $t_{32} = -2.18$, $p = 0.037$; Figure 1). The effect size (± variance) of sex was $g = -0.73 \pm 0.12$ (95% confidence interval: 0.02-1.44), indicating a large effect size (Cohen 1988).

Discussion

We found higher Hg concentrations in female Crested Auklets than males at Kiska Island, counter to the hypothesis that females' Hg burden should be lower as they can depurate Hg into their egg. Crested Auklets lay a single egg, weighing approximately 14 % of female body mass (260 g; Fraser et al. 1999; Jones 1993a). Previous studies that examined this hypothesis found that, though it was supported, depuration into eggs could not fully account for the differences in Hg between sexes (Ackerman et al. 2016a; Monteiro and Furness 2001). In some species, however, there is no significant relationship between Hg in females' winter-grown breast feathers, and Hg in their subsequent eggs, as the kinetics of Hg depend on the timing and pattern of feather moult (Ackerman et al. 2016a; Braune and Gaskin 1987a; Thompson et al. 1998).

The effect size of sex on feather Hg concentrations was in the 7th percentile of a recent review (Robinson et al. 2012), suggesting that our study is one of the few cases where the difference in feather Hg is so great between sexes and greater in females than males. This suggests either a dietary/physiological difference between the sexes, or spatial segregation resulting in differential Hg exposure. Male and female Crested Auklets' behaviour during the breeding differs markedly (Fraser et al. 2002; Wails 2016), and they are the most sexually dimorphic auk (Gaston and Jones 1998; Jones 1993b; Jones et al. 2000).

We would expect differences in feather Hg if females and males differed in either their exposure or physiology. During the non-breeding season, it is expected that Hg exposure (and therefore concentrations of Hg acquired) should be equal between the sexes as females are not laying eggs, and the physiological kinetics of Hg should be similar (Monteiro and Furness 2001). Crested Auklet breast feathers are likely grown in the early spring (Pyle 2008); males and females differ in body size and also bill shape and size – with the larger males having more strongly hooked bills in summer (Jones 1993b). Crested Auklet males and females take on different roles during chick-rearing, with a greater role for females in chick provisioning and of males in chick guarding (Fraser et al. 2002), with strong differences in diurnal timing of colony attendance between the sexes (Wails 2016). Crested Auklets are the only member of the family Alcidae for which individuals' sex can be determined by examination of external characters, and are the most sexually dimorphic auk (Gaston and Jones 1998; Jones 1993b; Jones et al. 2000). Male bill shape and size may be affected by intra- or intersexual selection because the bill is used for fighting as well as display (Gaston and Jones 1998) but the dimorphism could manifest in dietary differences between sexes (Mancini et al. 2013; Phillips et al. 2011), and therefore Hg exposure. Studies of Crested Auklet diet outside the breeding season are virtually unknown, save one specimen shot in January 1883 (Stejneger 1885), and a study of nine birds (2 adult males, 3 subadult males, 4 subadult females) collected in Unimak Pass in the winter of 1986-1987, which did not examine sex or age differences (Troy and Bradstreet 1991), though diet composition appears to be broadly similar to that of chicks in the breeding season, dominated by euphausiids (Bond et al. 2012). Why then did females in our sample have higher Hg? Hg in feathers could also represent some of the body burden acquired during the previous breeding season. Hg is eliminated via feathers from a body pool acquired several months previously. An understanding of non-breeding dietary differences between male and female Crested Auklets is lacking, and impedes our interpretation.

Sex differences in Hg could also arise from spatial segregation (Watanuki et al. 2016). Based on archival geolocation tracking data of birds from Buldir and Gareloi Island, Aleutian Islands between 2013 and 2015, significantly more females than males overwintered in the Kuroshio Current Large Marine Ecosystem (K. Robbins unpublished data). The Kuroshio Current Large Marine Ecosystem lies off the east cost of Japan (Di Lorenzo et al. 2013); Red-legged Kittiwakes (*Rissa brevirostris*) wintering in the Kuroshio Current had the highest feather total Hg concentrations (Fleishman et al. 2019). Streaked Shearwaters (*Calonectris leucomelas*) wintering in different areas of the Pacific Ocean showed considerable variation in feather Hg concentrations (Watanuki et al. 2016), and a similar pattern may be present in Crested Auklets.

Crested Auklet males and females do not differ significantly in crest length (i.e., they are sexually monomorphic for this ornament; Jones et al. 2000), even though females have a greater Hg burden. Notably, variability in crest size in Crested Auklets was found to be greater in females than in males (Jones et al. 2000). Feather Hg was also unrelated to the degree of measurement asymmetry of auklets' auricular plumes, another possible indicator of individual quality. One possible explanation is that the Hg concentrations we observed were too low to cause any negative physiological effects. Among piscivores, including many seabirds, Hg concentrations of >20 µg/g in feathers is the threshold at which when negative effects are likely to manifest (Ackerman et al. 2016b; Bond et al. 2015; Evers et al. 2014). Sublethal effects, however (such as ornament expression) are likely affected at lower concentrations, though the effect threshold is undoubtedly species specific; among birds, smaller species have lower Hg toxicity thresholds compared to larger species (Fuchsman et al. 2016). The maximum feather Hg concentration we measured was 1.69 µg/g; within individuals, Hg concentrations in feathers is typically greater than concentrations in blood, and though toxicity thresholds are highly variable (Ackerman et al. 2016b; Fuchsman et al. 2016), we conclude that Crested Auklets are not likely experiencing deleterious effects of Hg.

Our results indicate low concentrations of Hg in the feathers of a planktivorous seabird are unrelated to ornament expression, likely owing to the low concentrations we measured. Furthermore, we identified a significantly greater mercury burden in females compared to males that appears to be unrelated to expression of sexually selected ornaments, and was contrary to expectations, suggesting some unknown physiological or behaviour differences between sexes, which deserves further exploration. Measurement of Hg burden in feathers is not difficult or invasive, and should be considered as an add-on for future seabird tracking studies, as these birds are wide ranging top predators of the world’s oceans.

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Compliance with Ethical Standards

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This research was approved by the Memorial University of Newfoundland Institutional Animal Care Committee (protocol 09-01-IJ), and conducted under United States Federal Bird Banding Permit 22181, United States Fish and Wildlife Service Migratory Bird Permit MB176119-1, and Canadian Wildlife

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Tables

Table 1 – Candidate models for predicting Hg concentrations in Crested Auklet breast feathers ranked by Akaike's Information Criteria adjusted for small sample size (AICc), with differences from the top-ranked model (ΔAIC_c) and individual models' Akaike weights (w_i).

Model	**Parameters**	**AIC_c**	**ΔAIC_c**	**w_i**
Sex	3	31.95	0.00	0.730
Year	3	34.67	2.72	0.188
Sex × Year	5	36.52	4.57	0.074
Crest × auricular asymmetry	5	41.74	9.79	0.006
Sex × Year × auricular asymmetry	8	44.15	12.20	0.002
Sex × Year × crest	8	44.53	12.58	0.001
Sex × crest × auricular asymmetry	9	49.09	17.14	0.001
Year × crest × auricular asymmetry	9	51.67	19.72	<0.001
Sex × Year × crest × auricular asymmetry	14	69.67	37.72	<0.001

Figure Captions

Figure 1. Total mercury in Crested Auklet breast feathers (μg/g fresh weight) differed significantly between sexes. Solid lines are the median, boxes are the interquartile range, whiskers are 95% percentile, and dots are final outliers.