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Research paper

Egg size is independent of variation in pre-breeding feather corticosterone in Cassin's auklets during favorable oceanographic conditions

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ABSTRACT

The measurement of corticosterone levels in feathers (fCort) is gaining recognition as an effective means for describing links between stages of the annual cycle in birds. Many seabirds are especially good models for exploring these links, or carryover effects, due to their migratory behavior and reproductive investment in a single-egg clutch. Here, we measure fCort in Cassin's auklet (*Ptychoramphus aleuticus*) breast feathers at two colonies in British Columbia during 2011, a year of favorable oceanographic conditions, and examine its relationship with egg size. These feathers are grown at sea during the late winter period, 1–2 months prior to egg laying. Assuming that fCort provides some measure of nutritional stress and hypothalamic-pituitary-adrenal axis activity during feather growth, we predicted that fCort would be positively correlated with egg size via increased support for foraging activity during the nutritionally demanding molt stage. We also analyzed the $\delta^{13}C$ and $\delta^{15}N$ stable isotope content of breast feathers, measures commonly used to characterize seabird diet composition. Contrary to prediction, neither fCort nor stable isotope ratios were good predictors of egg size. Our results appear to conflict with two previous studies on alcids in which fCort and stable isotopes showed clear links with egg size; however, both studies were conducted in years when oceanographic and foraging conditions were poor. Under these conditions, upregulation of corticosterone may be needed to mediate the energetic tradeoffs between self-maintenance and reproduction, supporting increased foraging effort and thus increasing both the likelihood of reproduction and large egg size. However, when foraging conditions are favorable, we suggest that such tradeoffs and associated physiological constraints are minimized and regulation of egg size may be effectively independent of circulating corticosterone levels and diet type.

1. Introduction

Many contributors to lifetime fitness and population level processes, including variation in breeding propensity, reproductive success, and survivorship, can be influenced by carryover effects: features of an organism's current performance that are explained by its past experience (O'Connor et al., 2014). These effects can act across a variety of temporal and spatial scales and have been documented in many marine species, including seabirds (e.g. Harrison et al., 2011). The most commonly identified carryover effects on reproduction stem from non-breeding or pre-breeding body condition (Crossin et al., 2013b, 2012a; Harrison et al., 2011; Salton et al., 2015), winter habitat quality (Norris et al., 2004; Sedinger et al., 2011), diet (Inger et al., 2010; Sorensen et al., 2009), and physiologic state (Crossin et al., 2013b, 2012a, 2010; Kouwenberg et al., 2013). Each of these factors has been implicated in effects on breeding, including the decision to breed, reproductive phenology, and success, as well as levels of investment such as egg size and chick provisioning.

Since many carryover effects from the non-breeding period appear to be driven by environmental experience and nutritional stressors, physiologic state and diet are likely to be important indicators of these effects. Glucocorticoid hormones, including corticosterone (Cort), act as metabolic regulators of physiological and behavioral responses to unpredictable stressors (Hau et al., 2010; Wingfield et al., 1998), helping to regain positive energy balance in situations of allostatic overload (McEwen and Wingfield, 2003). These hormones are thus important components of pre-breeding physiologic state and have been identified as key mediators of many carryover effects.

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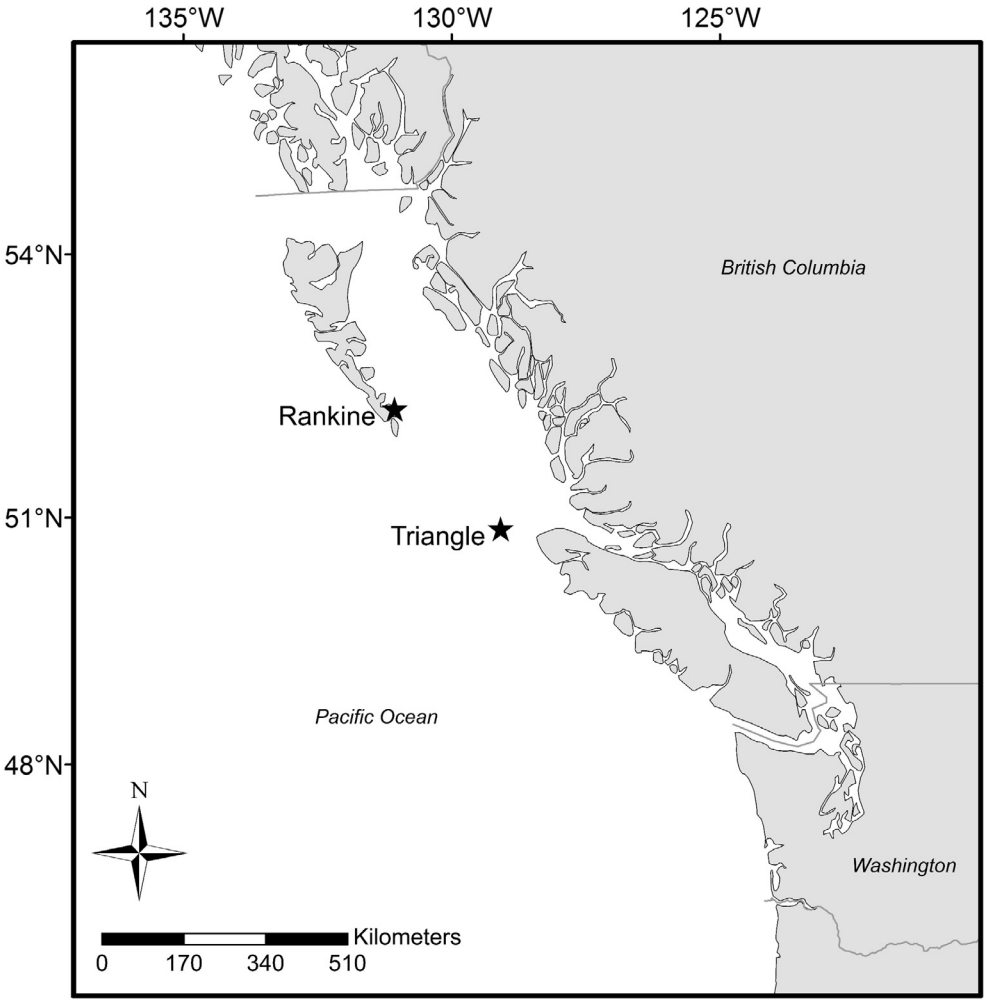

Fig. 1. Geographic location of the Triangle and Rankine Island study sites in British Columbia. Map generated using ArcMap 10.3 (ESRI, Redlands, CA, USA).

For seabirds, the measurement of Cort in feathers (fCort) has been a particularly useful way to examine longer term, cumulative Cort dynamics during the non-breeding period when most birds molt and grow new feathers (Bortolotti et al., 2009, 2008; Fairhurst et al., 2013). Similarly, feathers can be used to obtain integrated information on diet during the non-breeding period via stable isotope composition (Inger and Bearhop, 2008); 15-nitrogen is enriched in consumer tissues as trophic level increases (increasing $\delta^{15}N$) and 13-carbon exhibits an enrichment gradient from offshore to inshore prey sources and from pelagic to benthic prey sources (increasing $\delta^{13}C$) (Bond and Jones, 2009; Hobson et al., 1994; Kelly, 2000). Increases in fCort can be regarded as a direct physiological indicator of increased nutritional stress during periods of low food availability (Kitaysky et al., 2007; Will et al., 2015, 2014; but see opposite relationship in Patterson et al., 2015), and have also been linked to enhanced foraging effort, with positive effects on foraging success and reproductive investment (Crossin et al., 2012b; Kouwenberg et al., 2013). Feather Cort, $\delta^{15}N$, and $\delta^{13}C$ each provide unique information about non-breeding foraging experience and are useful tools for assessing the potential mechanisms governing carryover effects, particularly when examined together.

Seabirds share a suite of life-history traits across species, including high survival rates and low reproductive rates (Lack, 1968). Recent studies of these species have linked elevated pre-breeding fCort and diet quality to key fitness traits such as earlier laying and larger egg sizes (Kouwenberg et al., 2013; Sorensen et al., 2009), and have also demonstrated that elevated fCort can be associated with increases in foraging activity required to support successful reproduction (Angelier et al., 2008; Crossin et al., 2013a, 2012b). If Cort is elevated to stress-induced levels, however, anti-gonadotropic effects can ensue (Salvante and Williams, 2003; Sapolsky et al., 2000), possibly by altering protein and lipid metabolism to favor self-maintenance over reproduction (Wingfield et al., 1998) and by suppressing the release of luteinizing hormone (LH) and subsequent estrogenic pathways (Brann and Mahesh, 1991; Etches et al., 1984; Goutte et al., 2010). Elevated fCort has thus been linked to negative reproductive effects, including later arrival at the breeding colony, poorer body condition at arrival, and reduced reproductive success (Harms et al., 2015), as well as breeding deferral (Crossin et al., 2013a; Hansen et al., 2016). Although such effects are detrimental to current reproduction, they may benefit lifetime fitness by helping balance reproductive demands with maternal quality and nutritional state (similar to Love and Williams, 2008).

Here, we test the hypothesis that the pre-breeding physiologic state and diet of a sentinel seabird, the Cassin's auklet (*Ptychoramphus aleuticus*), as represented by feather Cort and stable isotope content, will carry over to affect breeding investment and performance in the form of egg size. Our study took place in a year with favorable oceanographic conditions, thus we did not anticipate any chronic elevations in Cort sufficient to inhibit reproduction. Using the single-egg clutch of the Cassin's auklet as a model, we predicted (1) that higher fCort levels and (2) lower $\delta^{15}N$ would be linked to larger egg size, due to increased physiological support for foraging activities during the nutritionally demanding molt stage and preferred, lower trophic level diet, respectively. Cassin's auklet mouth parts are adapted for zooplanktivory (Bédard, 1969) and, though non-breeding diet is not well understood,