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The prudent parent meets old age: A high stress response in very old seabirds supports the terminal restraint hypothesis

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ABSTRACT

The reproductive success of wild animals usually increases with age before declining at the end of life, but the proximate mechanisms underlying those patterns remain elusive. Young animals are expected to invest less in current reproduction due to high prospects for future reproduction (the "restraint" hypothesis). The oldest animals may also show restraint when conditions are sub-optimal where even a small increase in reproductive investment may lead to death ("terminal restraint"). Alternatively, reproduction may be constrained by lack of experience and senescence (the "constraint" hypothesis). In two species of breeding seabirds, behavioural (time to return the offspring, calmness during restraint) and physiological (metabolism, glucose and corticosterone) parameters responded similarly to stress with advancing age, implying a generalized stress response. Across those parameters, birds were "shy" (high stress response) when young or old, and "bold" (low stress response) when middle-aged. Specifically, free corticosterone, the principal avian glucocorticoid responsible for directing energy away from reproduction and towards immediate survival following stress, was highest in both young and very old stressed birds. All age groups had a similar adrenal capacity to produce corticosterone, implying that middle-aged birds were showing restraint. Because the stress response, was highest at ages when the probability of current reproduction was lowest rather than at ages when the probability of future reproduction was highest we concluded that birds restrained reproductive investment based on current conditions rather than potential future opportunities. In particular, old birds showed terminal restraint when stressed. Hormonal cues promoted investment in adult survival over reproductive output at both the start and end of life consistent with the restraint hypothesis.

Introduction

Life-history theory predicts that iteroparous organisms will reduce investment in current reproduction when costs to future reproductive output outweigh the benefits of current reproduction (Williams, 1957; Stearns, 1992). Young animals, in particular, are expected to invest less energy in reproduction as they have more subsequent chances to reproduce (the "restraint" hypothesis, e.g. Heidinger et al., 2006; Desprez et al., 2011). Increased investment in current reproduction as the probability of substantial future reproductive output decreases may in part explain why reproductive success usually increases with age (de Forest and Gaston, 1996; Newton, 1998; Lewis et al., 2006; Angelier et al., 2007; Coulson, 2011; Hypothesis 1). One potential mechanism to account for such patterns is reluctance by older birds to abandon reproduction during stressful situations such as reduced food availability or risk of predation (Heidinger et al., 2006, 2010; Wilcoxen et al., 2011; Goutte et al., 2011; Riechert et al., 2012; Elliott et al., 2014a).

The oldest animals may also show restraint in reproduction during stressful years because even a small increase in energy expended during reproduction may lead to death ('terminal restraint hypothesis'; McNamara et al., 2009; Heinze and Schrempf, 2012; Hypothesis 2). For instance, longevity may be limited by low physiological condition (high 'biological age') rather than high chronological age if death occurs after physiological condition is reduced beyond a minimum threshold (McNamara et al., 2009). If each reproductive event increases biological age, then lifetime reproductive success may be higher if old individuals, near their maximum biological age, forgo reproduction during stressful years, when biological age is increased by a greater degree than during non-stressful years, and only invest heavily in reproduction during non-stressful years (McNamara et al., 2009). The assumption that individuals base life-history decisions on biological age rather than chronological age is supported by several studies that have shown that telomere

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dynamics better predict longevity than chronological age (Haussmann et al., 2005; Pauliny et al., 2006; Bize et al., 2009; Salomons et al., 2009; Heidinger et al., 2012).

Alternatively, both very young and very old animals may lack the experience or physical capacity necessary to maintain high levels of energy intake (the "constraint" hypothesis; Hypotheses 3 and 4), leading to reduced reproductive success (Finkel and Holbrook, 2000; Costantini et al., 2012). Finally, higher reproductive success among older age classes may reflect the selective mortality of low-quality phenotypes that produce few offspring (Forslund & Pärt 1995; Hypothesis 5).

Many studies have observed an increase in reproductive success in long-lived animals with age followed by a reduction at the end of life (de Forest and Gaston, 1996; Newton, 1998; Lewis et al., 2006; Angelier et al., 2007; Coulson, 2011), but fewer studies have examined the proximate mechanisms, which can provide clear, testable predictions for each of the hypotheses explaining the ultimate causes of these patterns (Table 1). The endocrine stress response provides a mechanism through which the competing demands of life-history trade-offs can be regulated, including those between current versus future reproduction. Glucocorticoid hormones released in response to a stressful event shift energy investment away from reproduction and towards immediate survival (Wingfield and Kitaysky, 2002; Satterthwaite et al., 2010; Kitaysky et al., 2010; Schultner et al., 2013a,b). For instance, as their name suggests, glucocorticoids mobilize fuel stores and increase circulating glucose necessary to fuel the muscles during rapid movement, such as flight from a predator (Bateson and Bradshaw, 1997; Wingfield and Kitaysky, 2002). Older breeding individuals may secrete lower levels of glucocorticoids in response to a stress during breeding (Jessop and Hamann, 2005; Heidinger et al., 2006; Goutte et al., 2011). As one manner by which glucocorticoid hormones shift energy investment away from reproduction and towards adult survival is by increasing the propensity of an adult to desert its offspring and to reduce the rate at which the adult provisions its offspring, the net result of a lower glucocorticoid response can be to maintain investment in offspring during a stressful period (Lendvai et al., 2007; Goutte et al., 2011; Angelier et al., 2009; Kitaysky et al., 2010; Seltmann et al., 2012).

Although reduced levels of glucocorticoid hormones with age could represent restraint via increased investment in offspring during a stressful event when the probability for future reproductive success is low (Heidinger et al., 2006; Heidinger et al., 2010; Hypothesis 1, Table 1), alternative explanations exist. For instance, both young and very old individuals may show restraint and be more likely to abandon offspring in the face of a stressor because they are unlikely to successfully reproduce, as they are unable to forage adequately, have inadequate partners, obtain sub-optimal breeding sites or are otherwise inexperienced breeders (de Forest and Gaston, 1996; Newton, 1998; Lewis et al., 2006; Angelier et al., 2007; Coulson, 2011; Hypothesis 2). Alternatively, older individuals may have habituated to stress (Hypothesis 3) or senescence may cause deterioration in adrenal tissue (Hypothesis 4), both of which may dampen stress responses. Finally, reduced levels of glucocorticoid hormones among older age classes may reflect the selective disappearance of phenotypes with high stress responses (Forslund & Pärt 1995; Hypothesis 5). It is important to emphasize that these five hypotheses are not mutually exclusive and multiple mechanisms may operate simultaneously.

Table 1
Hypotheses tested in the current study.

Hypothesis	Prediction
1. Restraint for future opportunities	Stress response is proportional to residual reproductive success at a given age. Change only occurs in reproductive individuals.
2. Restraint when probability of current success is low	Stress response is inversely proportional to average reproductive success at a given age. Change only occurs in reproductive individuals.
3. Constraint via habituation	Stress response declines with age and is similar among reproductive and non-reproductive (pre-breeding) individuals.
4. Constraint via decay of adrenal tissue	Stress response declines with age and is similar among reproductive and non-reproductive (pre-breeding) individuals. Stress response declines with age following ACTH injection.
5. Selection against high-HPA individuals	Individuals with high stress responses have lower survival.

We examined these five hypotheses in two long-lived, cliff-nesting seabirds. We predicted that if Hypothesis 1 was true, then diminished response to a stressful event should be proportional to future reproductive potential and the stress response should exhibit the greatest suppression late in life, when future reproductive prospects decline rapidly due to the accelerating probability of mortality. If Hypothesis 2 was true, then the stress response should be inversely proportional to average reproductive success at any age, and the rate of diminishment of the stress response should be highest early in life, when reproductive success increases rapidly. We predicted that if Hypotheses 3 or 4 were true, then pre-breeding birds should show similar age-related trends in their stress responses as breeding birds. Glucocorticoids are secreted by the adrenal tissue in response to adrenocorticotropic hormone (ACTH), which is secreted by the pituitary gland. By first using the glucocorticoid receptor agonist dexamethasone to suppress natural production of ACTH (and therefore glucocorticoids), minimizing the confounding effect of endogenous ACTH release, and then exogenously injecting ACTH, we assessed the responsiveness of adrenal tissue (Astheimer et al., 1994; Boonstra et al., 2001; Schmidt et al., 2012). If Hypothesis 4, but not 3, was true, we predicted declines in glucocorticoid response to the ACTH challenges. Finally, if Hypothesis 5 was true, we predicted that individuals with high stress responses would have lower survival. To provide a stronger context for examining these relationships, we also examined behavioural and physiological adjustments occurring in tandem with the glucocorticoid response.

Methods

We studied pre-breeding (5 to 20 May 2012; N = 43) and chick-rearing (10 to 15 July 2010 and 12 to 20 July 2012; N = 89) black-legged kittiwakes *Rissa tridactyla* at Middleton Island, Alaska, and chick-rearing (20 to 31 July 2008 and 24 to 30 July 2011; N = 72) thick-billed murres *Uria lomvia* at Coats Island, Nunavut. We did not study pre-laying murres due to the difficulty of capturing those individuals. Kittiwakes had chicks 10–20 days old (fledging age averages ~40 days) and murres had chicks 3–10 days old (departure age averages ~20 days). Murres nested on a natural cliff (Gaston et al., 2005) while kittiwakes nested on an abandoned radar tower fitted with one-way glass that facilitated capture (Gill and Hatch, 2002; Hatch, 2013). We used primarily kittiwakes and murres banded as chicks and therefore of known age. However, as there were few very old birds, we included 14 kittiwakes banded as adults at least 10 years previously and three murres banded as adults at least 20 years previously. We added 5 years to the number of years since first capture to estimate their age (de Forest and Gaston, 1996; Vincenzi et al., 2013; Young et al., 2013). We captured murres by the neck using a noose pole and kittiwakes by the leg using a hook. To avoid reductions in stress response due to habituation to handling, we used murres that had likely not been handled since banded as a chick. For kittiwakes, we included years of handling as a covariate. We restrained birds by placing them in cloth bags that snugly fit the body. Only one adult per nest was captured. We did not correct body mass for linear size as such corrections do not improve estimation of lean or lipid mass in either murres or kittiwakes (Jacobs et al., 2012). For instance, in our kittiwake data set, body mass alone explains 92% of the variation in the residual of body mass on the first principal component of head-bill, tarsus, culmen and wing length, and consequently size-corrected mass explains little of the variation beyond mass alone. Murres were sexed using a combination of genetic markers and behavioural observations