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Selection on physiological traits is thought to mediate the evolution of individual life-history parameters like reproduction, longevity, and the tradeoffs between them, but almost nothing is known about the relationships between physiological and life-history parameters in the wild. Antioxidants are strong candidates to correlate with life histories because they play a critical role in preventing free radical damage to macromolecules, and many types are involved in sexual signaling and embryo provisioning. Here for the first time we present data on associations between serum antioxidant measures (antioxidant capacity and concentrations of uric acid, vitamin E and carotenoids) and indices of reproductive rate and age in two bird species. After controlling for age, 36% of the variation in hatching rate in Leach's storm-petrels *Oceanodroma leucorhoa* was accounted for by a negative association with antioxidant capacity. Age was negatively associated with uric acid levels. Savannah sparrows *Passerculus sandwichensis* showed no association between antioxidant capacity and fledging rate, but serum β-carotene levels were weakly positively associated with fledging rate. Because antioxidant levels are known to vary markedly within individuals over time, detection of associations between long-term measures of reproduction and instantaneous antioxidant levels suggests strong (though not necessarily causal) relationships. Relationships between antioxidants and life histories appeared to differ in sparrows and storm-petrels though, likely due to variation in diet, ecology, and life-history evolution in these distantly related species.

Evolutionary ecologists have long had an interest in understanding the tradeoffs between reproduction and longevity, i.e. current versus future reproduction (Williams 1957, Stearns 1992). Although some studies have investigated the role of hormones in regulating behavior that affects these tradeoffs, very little is known about more direct physiological causes and consequences of the tradeoffs (Ketterson et al. 1996, Ricklefs and Wikelski 2002). Why does reproductive effort incur physiological costs, and would understanding these mechanisms help explain why some species appear to be more likely than others to increase toward understanding whether and how oxidative balance may help mediate life-history tradeoffs.

Physiological systems are complex, and antioxidants are an imperfect measure of oxidative balance. Much of the important variation may be due to regulation of the rate of free radical production, although it appears that antioxidants may respond to need, such that high levels indicate greater oxidative stress (Lopez-Torres et al. 1993, Brand 2000). Antioxidant systems also vary greatly across tissues and across species. In many tissues, and primarily in mitochondria, antioxidant enzymes are the key defense against oxidative damage (Barja 2004). In circulating systems (measured in this study), micromolecular antioxidants such as uric acid, vitamins C and E, and carotenoids play a more important role (Miller et al. 1993). Antioxidant enzymes, which have a specialized function, are likely regulated to adjust antioxidant protection specifically, whereas micromolecular antioxidant levels depend on dietary intake and on their other physiological roles such as signaling. Additionally, the diverse roles of micromolecular antioxidants mean that different trends might be seen for different types of antioxidants. In particular, carotenoids are important in sexual signaling and immune function, making it possible that carotenoids would correlate positively with reproductive rate even while other types of antioxidants might correlate negatively, particularly if reproductive rates reflect quality and high antioxidant levels reflect high oxidative stress (Bortolotti et al. 2003, McGraw 2006). Across species, variation in diet and in other aspects of physiology mean that antioxidants may vary for reasons unrelated to life-history tradeoffs (Tella et al. 2004).

We assessed the relationship between circulating antioxidant concentrations and age and reproductive rate in two species that have been studied at the same site for many years: Leach's storm-petrel taken within 3 min of capture to avoid effects of the hypothalamo-pituiary-axis-activated stress response on antioxidant concentrations (Cohen et al. 2008a). Trolox-equivalent antioxidant capacity (TEAC) of serum and uric acid were measured using spectrophotometric methods following Cohen et al. (2007). Vitmain E and carotenoids were measured using HPLC following previously published methods (McGraw and Parker 2006). Details of these methods can be found in the Supplementary material Appendix 1.

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In both study species, reproduction is higher in older birds; in the petrels this is apparently due to higher mortality of low-quality individuals at young ages (Wheelwright and Schultz 1994, Mauck et al. 2004). However, in many species there is also evidence for a tradeoff between reproduction and survival, or old individuals may be senescent (Daan et al. 1996). The positive association between reproduction and age in our species allows us to use a measure of reproduction – average annual offspring production, up to current age, or ‘reproductive rate’ – that would be confounded by a tradeoff or by strong effects of senescence in other species. We could not use lifetime reproductive success, which includes all offspring produced in a lifetime, because most of our individuals were not near the end of their lifespans. Because we did not have data on fledging for many Leach’s storm-petrels, we used the percentage of all eggs that hatched up to present during these data were always separated for analysis. One night-caught bird was an outlier with high TEAC (4.16, = mean + 6.2 SD) and low Res (−1.19, = mean −8.7 SD) and was excluded from all analyses of these variables. (These standard deviations were calculated excluding the outlier. If it is included, they become 2.9 and 3.2 SDs from the mean respectively.) Only two carotenoids, lutein and zeaxanthin, were detected in Leach's storm-petrels. All measures of antioxidants except possibly lutein differed markedly between day and night, with much higher values at night (Table A1). Day- and night-caught birds did not differ in body size. Correlations among antioxidants are shown in Fig. 1, but are not strong or general enough to justify multivariate characterization of antioxidants (Cohen and McGraw 2009).

In day-caught birds, average annual reproductive rate was negatively associated with TEAC (Fig. 2) and with UA after controlling for breeding age, but was not associated with Res, vitamin E concentration, or concentration of either carotenoid (Table 1). The TEAC association remained significant when the lowest-reproducing individual (0% success) was excluded ($p = 0.04$), and when we weighted for breeding age (our effective sample size, $p = 0.007$). Results were identical to correlations without age adjustment (data not shown). There was a clear negative correlation between age and UA (Fig. A1) and a marginal one between age and Res, but other antioxidant measures were unassociated with age or body size in Leach's storm-petrels (Table 1).

Five carotenoids – lutein, zeaxanthin, β-cryptoxanthin, β-carotene, and α carotenoids, β-carotene would be the one associated with individual life-history parameters. It is an important vitamin A precursor and tends to be limiting in the xanthophyll-rich diets of granivores (Goodwin 1980, 1984). β-carotene is present in Savannah sparrows at much lower levels than any of the other carotenoids, consistent with a limiting role in

If associations between antioxidants and reproductive rate are generally dependent on life history strategy, long-lived species may have higher reproduction when overall anti-oxidant levels are low. In contrast, in shorter lived species, many of which have carotenoid-rich diets, reproductive rate physiology evolves to rely on it, and it may eventually be incorporated into sexually selected signals. Conversely, foraging habits may also evolve in response to physiological need. In addition to the interplay between diet and physiology, there should be selection in response to tradeoffs (along the r–K continuum, for example). But because of the diverse ways that the diet can interact with multiple physiological alternatives, the consequences of this selection on physiological systems (and thereby on antioxidant levels) could vary widely across taxa. A proper understanding of these issues will require much further study, in particular a combination of experimental and comparative approaches tailored to elucidate causes and consequences of variation in antioxidant levels or other aspects of physiology, and how these associations vary across species.

The Supplementary material Appendix 1 contains additional discussion of antioxidant differences by time-of-day in petrels and depending on breeding status in sparrows.

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