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The role of ecological tradeoffs in the evolution of endocrine function

Animals in the wild are faced with making decisions every day that can impact their reproductive fitness and survival. Obviously successful reproduction and maintenance of energy balance are critical for health and survival in all animals, but these processes must be balanced with avoidance of predators, preparation for seasonal changes in weather, and defense against unpredictable environmental events that may adversely impact survival and fitness.

Research over the last three decades supports the hypothesis that endocrine systems controlling stress, feeding, reproduction, and growth respond to selection pressures such as predation, unexpected natural disasters and weather events, and anthropogenic pollution. The aim for this volume was twofold. The first aim was to review the evidence that ecological tradeoffs lead to changes in endocrine function in animals in their natural habitat. The second aim was to address the possibility that ecological tradeoffs (such as foraging/predator avoidance and reproduction/predator avoidance tradeoffs) have shaped evolution of the endocrine axes controlling stress, feeding, reproduction, growth, and development.

This special issue contains 14 manuscripts (8 empirical studies, 6 reviews) spanning a wide range of vertebrates. The papers tackled several tradeoffs including: current vs. future reproduction; self-maintenance/survival vs. reproduction; feed vs. flee; vigilance vs. foraging; cooperation vs. competition. The majority of papers (11/14) addressed the role of hypothalamus-pituitary adrenal (HPA) axis function, at least partially, in ecological, behavioral, and physiological tradeoffs. Authors also investigated the role of other hormones, including thyroid hormones, androgens, estrogens, energy metabolites (e.g., glucose, fatty acids), oxytocin, prolactin, and neuropeptide Y. The broad discussion of the role of the HPA axis in tradeoffs is not surprising given its role in many physiological and behavioral processes and its evolutionary conservation across vertebrate taxa.

The presence of challenges or stressors (e.g., predator cues, inclement weather, food availability) often activates the HPA axis, and thus increased HPA axis activity, including corticotropin-releasing factor and glucocorticoid (GC) release, may be adaptive in multiple tradeoffs. Some have speculated that GCs direct behavior and physiological changes that optimize the response to predators and underlie predator-avoidance tradeoffs (Harris and Carr, 2016). Many others have shown the HPA axis, and GCs, mediate several life-history tradeoffs, including immediate survival over reproductive effort (Crespi et al., 2013; Wingfield and Sapolsky, 2003). Fittingly, in a capstone review paper for this special issue, Harris (2020) defines and organizes 131 different hypotheses or models that make predictions about the role that the HPA axis, stress, and/or the sympathetic nervous system play in tradeoffs, transitions, and organismal health. Harris found that out of the published hypotheses/models dealing broadly with stress and tradeoffs or transitions, the majority are related to reproduction, followed by the transition from health to disease, developmental transitions, and stress coping. Harris' review also highlights the importance of reproducibility and choosing hypotheses *a priori* to prevent hypothesizing after results are known (HARK-ing). Lastly, it provides some practical concerns, considerations, caveats, and recommendations for robust testing of stress- and HPA-related hypotheses.

Relatedly, Lattin and Kelly (2020) tackle the importance of GC negative feedback in survival/reproduction tradeoffs and highlight the need for consistent testing and reporting of data. They scanned 567 published studies for relevance and chose 75 to catalog, compare, and contrast seven common approaches used to calculate negative feedback following dexamethasone challenge. Next, they re-analyzed an existing dataset using the seven different methods. Importantly, theyfound that not all calculations of negative feedback yielded the same pattern or interpretation of the dataset. Based on their calculations and comparisons, Lattin and Kelly recommend that authors present negative feedback data as relative reduction from stress-induced GCs. Lastly, Lattin and Kelly (2020) tested six specific predictions about GC feedback both across (life history strategy, length of breeding season, and type of parental investment) and within (body condition of the parents, age of the breeding animals, and the costs of abandoning offspring) individuals. Overall, they conclude that few studies have tested all six predictions but that the available data suggest that poor body condition correlates with weak glucocorticoid feedback in breeding animals.

Obviously, there are constraints with any animal model system or study on natural populations that can result in uncertainty about extrapolating a single dataset across groups. With respect to stress and the influence of the HPA axis on tradeoffs, these limitations include the type of stressor, time of day, and whether repeated sampling is possible. Grant et al. (2020), studying mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*), compared repeated sampling of baseline and stress-induced corticosterone and baseline testosterone levels over time (3 months) and space (home range) to determine if hormone phenotype related to nesting success. Of central importance to this study was the repeatability of the hormone findings over time. The authors report that while population-level stress-induced increases in blood corticosterone were repeatable over time for males, baseline corticosterone and blood testosterone were not, suggesting that single point measurements may not represent underlying endocrine status. Grant et al. (2020) report that males with a greater stress-induced corticosterone had more central home-ranges. They also report that while males in better body condition had larger home-ranges, but home-range size did not relate to hormone concentrations or nesting success. Overall, variation in hormone levels did not influence nesting success.

The long-term effects caused by early developmental exposure to stressors is an active area of stress endocrinology, but most studies to

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date have focused on laboratory rodents. Grace et al. (2020) take these questions into the field in a controlled exposure study using house sparrows (*Passer domesticus*). Grace et al. (2020) dosed wild, free-living nestlings with corticosterone-containing mealworms and then fledglings were transferred to captivity and the GC response to a previously standardized capture-restraint protocol was tested at the pre-fledging, juvenile, and adult stages. Grace et al. (2020) report that early-life GC manipulation was associated with depressed baseline and stress-induced concentrations of blood GCs at all test periods through to adulthood. The resutls broadly support the Match-Mismatch Hypothsis and suggest that early-life exposure to elevated GCs might prime individual phenotype for a challenging adult life, and prioritize reproduction at the cost to self maintenace. Thus, early developmental exposure to a stressor can have long-term effects on an endocrine system known to modulate ecological trade-offs (Harris and Carr, 2016).

Hudson et al. (2020) examine the interplay between GCs and reproduction vs self-maintenance (energetic state, immunocompetence) in a parthenogenetic (all female) lizard species, Colorado Checkered Whiptail (*Aspidoscelis neotesselata*), by investigating associations between blood estradiol and corticosterone measures with metabolic (glucose, triglycerides, glycerol) and immune system (bactericidal activity of plasma) markers. The authors report evidence for changes in physiological investment across reproductive contexts in this lizard species. Specifically, patterns of sex and metabolic hormones (plasma estradiol and corticosterone, respectively) varied with blood immune and metabolic markers varied across seasons and vitellogenic state (active, inactive). Blood corticosterone levels were inversely associated with reproductive activity as well as immunocompetence.

Pritchard et al. (2020) examine the potential associations between two important metabolic hormones, GCs and triiodothyronine (T3) and state-dependent foraging/predator avoidance tradeoffs in two wild populations of vicuña (*Vicugna vicugna*). Their study populations varied in habitat quality and exposure to predators (Puma, *Puma concolor*), providing an excellent natural experiment on hormonal correlates of foraging/predator avoidance tradeoffs. Pritchard et al. (2020) report differences in foraging and vigilance behaviors between the two vicuña populations, although fecal GC metabolites and fecal T3 did not correlate with the behavioral differences between sites. The authors suggest that small tradeoff-related changes in behavior may not require changes in adrenal and thyroid hormone secretion large enough to be detected in fecal samples.

Islam et al. (2019) also tackle a foraging-related question by revisiting Ewert's hypothesis that neuropeptide Y (NPY), originating from neurons in the visual thalamus, inhibits tectal responsiveness to prey items. They report that while NPY microinjections into the optic tecta produced a dose-dependent trend toward reduced food intake, they did not significantly inhibit over all food intake by juvenile South African clawed frogs (*Xenopus laevis*). NPY at the largest dose did alter discrete prey-capture behaviors, causing frogs to eat their food more rapidly. These effects were mediated via tectal Y2 receptors as they were blocked by the Y2 selective antagonist BIIE0246. Interestingly, blockade of tectal Y2 receptors prevented some of the antipredator behaviors exhibited by juvenile frogs to a conspecific predator (*X. laevis* are anurophagic, Measey 1998, Measey et al., 2015). Collectively these findings support the hypothesis that NPY may act as a circuit breaker, disrupting appetitive behaviors in favor of avoidance behaviors (Islam et al., 2019).

In addition to its role in feed/flee tradeoffs, the HPA axis responds to anthropogenic and parasitic stressors (Lindsay et al., 2016), and likely aids in coordinately and influencing organismal response to these challenges, although the response to anthropogenic stressors is not consistent across species or stressors (Dantzer et al., 2014). For example some studies find no relationship between urbanization (and presumably everything that comes with that including roads, noise, pollution) and markers of HPA activity (e.g., baseline and stress-induced corticosterone release, Ibáñez-Álamo et al., 2020; Injaian et al., 2020) while at least one study has reported depressed plasma corticosterone associated with traffic noises (Zollinger et al., 2019). In this issue Malisch et al. (2020) provide evidence for an unusual relationship between habitat encroachment and stress in desert iguanas, *Dipsosaurus dorsalis*. They find that iguanas living closest to the roads have lower baseline corticosterone levels (but not lower post-stressor levels), which are associated with greater body condition and greater population density, suggesting that elements of this anthropogenic disturbance may be beneficial to the lizards by increasing vegetation due to water run-off.

Blévin et al. (2020) investigate the relationship between corticosterone, prolactin, poly- and perfluoroalkyl substance (PFASs) contaminants, and egg manipulation in wild black-legged kittiwakes (*Rissa tridactyla*). The authors build on data from their previous work and show that in female, but not male, kittiwakes egg angular change was positively related to plasma prolactin levels. There was no relationship between prolactin and egg turning behavior in either sex. Interestingly, the females with the highest blood PFAS (linearized PFOS and PFNA) concentrations turned their eggs more frequently and with a greater angular change; PFASs were positively related to prolactin levels in females. There was no association among corticosterone and behaviors in either sex. It is possible that environmental contaminants may provide some benefit for egg-care behavior in female kittiwakes, possibly mediated via plasma prolactin, and could play a role in the trade-off between parental care and foraging/self-maintenance. However, repeated sampling and PFAS manipulation studies are needed to determine cause and consequence.

Fernandez-Ajo et al. (2020) investigate the impact of Kelp Gull (*Larus dominicanus*) parasitism on Sothern Right Whale (*Eubalaena australis*) calves off the coast of Argentina. Kelp gulls in this region have developed a unique behavior where they feed on the skin and blubber of whales when they surface, and this has likely impacted whale populations in the region. Fernandez-Ajo et al. collected post-mortem baleen samples and degree of wounding from 36 calves that were found dead in the wild and analyzed the baleen for concentraiton of GCs and T3. They report that right whale calf (GC) levels positively correlated with degree of wounding but T3 did not. Thus, gull wounding may be a contributor to calf mortality in this region.

Two review papers in this issue tackle the role of endocrine systems on the evolution and maintenance of social behavior. Specifically, Olazábal and Sandberg (2020), review evidence related to oxytocin receptor density and social and reproductive strategy in rodents, while Vernasco and Moore (2020) review the evidence that testosterone mediates some of the tradeoffs between cooperation and competition.

Olazábal and Sandberg (2020) provide evidence that the differences in oxytocin receptor (OXTR) density in the lateral septum and nucleus accumbens (NAc) influences different reproductive and social strategies in wild and artificially selected populations of rodents. For example, higher density social groups and high levels of promiscuity are associated with smaller populations of OXTR in the NAc and LS while smaller social groups with lower levels of promiscuity (greater mate fidelity) are characterized by larger OXTR densities in the NAc and the LS. These findings are relevant to an understanding of the tradeoffs between monogamous and polygamous reproductive strategies.

Vernasco and Moore (2020) review the evidence that testosterone mediates some of the tradeoffs between cooperative breeding and competition for reproductive mates, which are generally considered to be at opposite ends of the same behavioral spectrum. That is, while both behavioral strategies have their benefits to long-term reproductive success, one must be suppressed for the other to emerge. The well-known role for testosterone mediating competitive behaviors makes it a candidate for directing the switch from cooperative to competitive behavior in the short term. However, at the individual, as opposed to the population, level less is known about the role that testosterone plays in mediating behavioral strategies. The authors provide some specific case study examples to address this gap. Data from meerkats and manakins support the hypothesis that testosterone levels mediate the tradeoff between cooperation and competition, and that understanding the role of individual variation in hormone and behavior relationships is critical.

Related to the topic of reproductive tradeoffs, Leary and Baugh (2020) review the relationship between GC levels, stress responsiveness, and sexual advertisement. They remind readers that while GCs can reduce investment in reproductive effort, such a generalized conclusion is not consistent with data. Aspects of GC action, including metabolic changes, are required for some aspects of reproductive effort and can facilitate reproduction. In their review, Leary and Baugh (2020) combined data from 54 studies reporting information on male traits and either endogenous or manipulated GC levels. The authors report that in studies where GCs are manipulated, the steroid hormones tend to reduce the attractiveness of male sexual advertisements to females. However, the relationship between male sexual signals and GCs is highly variable. Although there are fewer studies in females, their review suggests that research to date is consistent with high GC levels moderately dampening female proceptivity to male sexual advertisements or relaxing female choosiness, but more data are needed. Careau et al. (2020) hypothesized that the degree of reproductive investment would impact the consistency of metabolic and behavioral responses to an acute novel environment stressor in male zebrafinches (*Taeniopygia guttata*). The authors measured individual changes in blood corticosterone and temporal reaction norms in behavior and metabolic rate before and after seasonal reproduction. The authors report no statistically significant relationship between reproductive success (number of offspring fledged) and the slope and intercept of reaction norm responses to the stressor. Thus, in this study the immediate results of reproductive effort did not seem to alter stress responsiveness.

Overall, the manuscripts in this special issue provide considerable insight into the role the endocrine systems play in ecological, behavioral, and life history tradeoffs. A common theme in these papers is that when it comes to comparative endocrinology studies consistency in methodology, collection, analysis, and reporting of data are key. It is also clear that individual-, population-, and species-level differences are important for interpretation of data, and that stability of hormone-behavior relationships can be influenced by multiple biotic and abiotic factors.

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