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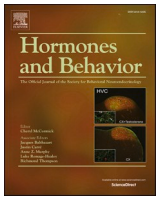

Editorial

Introduction to the Special Issue "Hormones and Hierarchies"

The relationship between social status, hormones, and behavior has been an active area of research since the 1980s. Many of the earliest studies in field endocrinology examined how hormone concentrations differ based on status within the hierarchy of a social group. As the field continues to grow, expanding across methods, approaches, and study systems, we thought it timely for an updated synthesis of past and ongoing work. This Special Issue features 17 articles capturing the diversity of the study of hormones and hierarchies.

The issue is anchored by Creel's review of foundational work on cooperatively breeding social carnivores (Creel, 2022). Beginning with studying dwarf mongoose (*Helogale parvula*) in Serengeti National Park in 1987, to African wild dogs (*Lyacon pictus*) in Selous Game Reserve in 1991, to wolves (*Canis lupus*) in Yellowstone National Park in 1999, Creel reviews the major findings of his and colleagues' pioneering work on the behavioral endocrinology of these species, as well as the creative methods developed to collect these data. Integrating these findings with recent work, he concludes that female reproductive suppression is often mediated by inhibition of the reproductive axis, while male reproductive suppression is more often mediated by behavior, with infanticide risk underlying this sex difference.

Along with the species highlighted by Creel, particular study systems have been key in understanding the physiological underpinnings of hierarchal social dynamics. Three such study systems are reviewed in this issue. First, Mustoe reviews the behavior and endocrinology of social dominance in cooperatively breeding callitrichid primates (Mustoe, 2023). Second, Drea and Davies review the endocrinology of female dominance and reproductive suppression in meerkats (*Suricata suricatta*), with a particular focus on androgens (Drea and Davies, 2022). Third, Maruska and colleagues review the endocrine and neuroendocrine correlates of male dominance in several species of African and Neotropical cichlids (Maruska et al., 2022).

As featured in these reviews, much work on the endocrinology of social dominance has focused on glucocorticoids, especially within the conceptual framework of the "cost of dominance" or the "stress of subordination." Dantzer and Newman take this framework in new directions by reviewing how social hierarchies among siblings and between species may influence the stress axis (Dantzer and Newman, 2022). Siblings within the same nest or litter often compete for resources provisioned by the parents, establishing hierarchies where dominants may have better resource access. Similarly, different species may compete for access to the same resources or influence the populations of mutual predators. Dantzer and Newman find that, though there is variation, there is more evidence for the stress of subordination in these contexts, and propose experiments to explicitly test this. Further expanding upon the relationship between social interactions and the stress axis, Lemonnier and colleagues summarize key physiological functions that are influenced by social stress, and may ultimately affect individual fitness (Lemonnier et al., 2022). These include metabolism, oxidative stress, inflammation, cognition, and biological rhythms. The authors highlight a need for greater cross-talk between ecological and biomedical researchers.

In addition to steroid hormones, there are other hormonal changes associated with social status. In cooperatively breeding mole-rats, prolactin is potentially a mediator of reproductive suppression in subordinate individuals. Hart and colleagues demonstrate that, in the Mahali mole-rat (*Cryptomys hottentotus mahali*), subordinate females have plasma prolactin concentrations that are as high as those of breeding females (Hart et al., 2022). Because these subordinate females are non-reproductive, the expectation is that they should have low or undetectable levels of prolactin. However, since their prolactin levels are elevated, seemingly without biological reason, this increase may be a proximate mechanism of reproductive suppression. Gilbert and colleagues directly test this hypothesis in naked mole-rats (*Heterocephalus glaber*), where similarly, non-reproductive subordinate females display elevated prolactin concentrations (Gilbert et al., 2022). They treat subordinate naked mole-rats with an anti-prolactin drug, Cabergoline. Surprisingly, Cabergoline treatment is not able to reduce prolactin levels in naked mole-rats, unlike in other mammals. This raises the question of what physiological pathways result in elevated prolactin levels in subordinate naked mole-rats, and it is still unclear if prolactin plays a direct role in subordinate reproductive suppression.

Beyond circulating hormonal changes, social status can also be linked to changes in gene expression related to endocrine or neuroendocrine activity. Lee and colleagues investigate this in male mice, socially classified as alpha, subdominant, or subordinate (Lee et al., 2022). They find that, in the medial preoptic area and ventral hypothalamus, transcriptional profiles differ across the three social statuses, particularly relating to genes involved with feeding/metabolism. Further, the subdominant males have increased expression of oxytocin and vasopressin in the medial preoptic area, relative to the alpha and subordinate males. In the social cichlid, Burton's mouthbrooder (*Astatotilapia burtoni*), Solomon-Lane and colleagues examine if social hierarchy rank among juvenile cichlids can be altered with vasopressin treatment, and the effects on whole-brain gene expression (Solomon-Lane et al., 2022). After treating juveniles with vasopressin, a vasopressin receptor antagonist, or a control injection, they find that these treatments do not alter the treated individuals' behavior, but do alter how the other fish in the group interact with it. Vasopressin receptor expression increases overall in groups where an individual has been treated with vasopressin, relative to groups where an individual has been treated with an antagonist.

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In the field, Bentz and colleagues look at ovarian transcriptome changes in response to social competition in tree swallows (*Tachycineta bicolor*; Bentz et al., 2022). By manipulating available nesting sites, they increase social competition in female swallows and find that 48 h after manipulation, expression of hydroxysteroid 17-beta dehydrogenase 1 is elevated in the ovaries. This enzyme is involved in androgen synthesis, and may potentially be related to how females in high competition environments allocate more androgens to egg yolks.

Social status is associated with behavioral differences, and these behaviors, in turn, are often associated with endocrine underpinnings. The last set of papers in this special issue focus on this topic. Roth and colleagues examine the relationship of territorial scent marking behavior and glucocorticoid levels in lactating female Columbian ground squirrels (*Urocitellus columbianus*; Roth et al., 2022). They find that ground squirrels increase vigilance after exposure to conspecific scents, but this increase is more pronounced when they are exposed to the scent of kin relative to the scent of unfamiliar individuals. Plasma cortisol concentrations increased only after exposure to kin scents, and this was particularly pronounced when these matrilineal females were exposed to the scent of their mother. Friesen and colleagues also test behavioral and endocrine responses to an intruder, in a very different study system (Friesen et al., 2022). Using Burton's mouthbrooder, they quantify behavioral, cortisol, testosterone, and neural activation changes in resident, dominant males exposed to a challenger male. They find that these changes in the resident male are context-dependent: they differ based on whether the intruder successfully secures dominance or becomes subordinate.

In another example of status-dependent aggression, Toor and colleagues study the endocrinology of subordinate behavioral phenotype in naked mole-rats (Toor et al., 2022). Within naked mole-rat colonies, there is a dominant, reproductive “queen” and dozens to hundreds of subordinates, however, these subordinates are not behaviorally homogenous. Older, higher ranked individuals tend to be more aggressive to unfamiliar animals, or “soldiers,” whereas younger, lower ranked individuals are “workers.” Non-aggressive animals that attempt to leave the colony, or “dispersers” are found to be scattered among age and ranking. Yet, Toor and colleagues find no particular endocrinological underpinning to these behavioral groups: testosterone, estradiol, progesterone, and DHEA are generally similar among types. Similarly, in green anole lizards (*Anolis carolinensis*), Kabelik and colleagues find that boldness in male anoles does not correlate with any steroid hormones measured, including testosterone, estradiol, progesterone, and glucocorticoids (Kabelik et al., 2022). However, they demonstrate that baseline vasopressin activity is lower in the paraventricular nucleus and supraoptic nucleus of males that are bolder towards other males.

In further behavioral studies, Martín-González and colleagues look at the association between compulsive drinking behavior, social dominance, and corticosterone in rats (Martín-González et al., 2022). Rats that are classified as high drinkers tend to lose more encounters in a social dominance test, and have delayed corticosterone responses, relative to the low drinkers. Finally, Smeltzer and colleagues review how social status relates to an unexpected behavior: sleep (Smeltzer et al., 2022). Where an individual ranks in a social group can be predictive of their sleeping positions, with higher ranked individuals sleeping centrally and having better thermoregulation and protection from predators. Smeltzer and colleagues discuss how these status-dependent sleep conditions may ultimately relate to stress and fitness.

Using a variety of methodologies and study systems, these articles highlight the marked endocrine and behavioral effects of social status. This body of work synthesizes the strong foundation of data on this topic, and where the field is going next. We thank Cheryl McCormick for facilitating this Special Issue, as well as the authors and reviewers for contributing their time and expertise.

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