Endocrine and neuroendocrine regulation of social status in cichlid fishes

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ABSTRACT

Position in a dominance hierarchy profoundly impacts group members' survival, health, and reproductive success. Thus, understanding the mechanisms that regulate or are associated with an individuals' social position is important. Across taxa, various endocrine and neuroendocrine signaling systems are implicated in the control of social rank. Cichlid fishes, with their often-limited resources of food, shelter, and mates that leads to competition, have provided important insights on the proximate and ultimate mechanisms related to establishment and maintenance of dominance hierarchies. Here we review the existing information on the relationships between endocrine (e.g., circulating hormones, gonadal and other tissue measures) and neuroendocrine (e.g., central neuropeptides, biogenic amines, steroids) systems and dominant and subordinate social rank in male cichlids. Much of the current literature is focused on only a few representative cichlids, particularly the African *Astatotilapia burtoni*, and several other African and Neotropical species. Many hormonal regulators show distinct differences at multiple biological levels between dominant and subordinate males, but generalizations are complicated by variations in experimental paradigms, methodological approaches, and in the reproductive and parental care strategies of the study species. Future studies that capitalize on the diversity of hierarchical structures among cichlids should provide insights towards better understanding the endocrine and neuroendocrine mechanisms contributing to social rank. Further, examination of this topic in cichlids will help reveal the selective pressures driving the evolution of endocrine-related phenotypic traits that may facilitate an individual's ability to acquire and maintain a specific social rank to improve survival and reproductive success.

1. Introduction

Dominance hierarchies typically occur when there is competition for limited resources like mates, food, or shelter/habitats. Dominance was initially defined as an attribute of the pattern of repeated agonistic interactions between two individuals, characterized by a consistent outcome in favor of the same dyad member and a default-yielding response of its opponent rather than escalation (Schjelderupp-Ebbe, 1922). Thus, the status of the consistent winner is dominant and that of the loser subordinate, but dominance is a relative measure and not an absolute property of individuals. While the definition of dominance sometimes varies and is still an area of debate (Drews, 1993), it is most commonly related to agonistic behavioral interactions. Nevertheless, social rank is established and maintained by frequent social interactions among individuals in the population, and this rank is associated with differences in behavior and physiology. Dominant individuals at the top of the hierarchy often have better health, more access to resources, and

higher reproductive success compared to lower ranking individuals (Sapolsky, 2005; Wingfield and Sapolsky, 2003; Zhou et al., 2018). Hormones also differ with social status, however, the specific roles that various hormones play in determining or maintaining an individuals' social status are not well understood in most species. Because social rank has such important survival and reproductive consequences, integrative and comparative studies on the mechanisms that control or are associated with social status are important. More than half of all vertebrate species are fishes, so examining dominance hierarchies in this diverse group is crucial for understanding the evolution of behaviors and regulatory control mechanisms that underly hierarchical societies.

1.1. Cichlids as important models for studying the hormonal and neuroendocrine basis of dominance

Cichlids (family Cichlidae) are a geographically widespread group of teleost fishes comprised of African, Neotropical, and Malagasy/Indian

clades (Friedman et al., 2013). Their remarkable mating systems (e.g., monogamy, polygamy), parental care strategies (e.g., mouthbrooding, maternal, paternal, biparental, cooperative), and alternative reproductive tactics (e.g., sneaking, piracy) even within closely related species makes them champions of diversity and evolution (Balshine-Earn and Earn, 1998; Kidd et al., 2012; Kuwamura, 1986; Sefc, 2011). Many species naturally live in complex and dynamic social societies with often limited resources such as shelter, food, and mates that leads to competition. As a result, dominance hierarchies are common in one or both sexes, making them excellent subjects for testing hypotheses on the role of hormones in establishing or maintaining social rank. Cichlids are also relatively easy to socially manipulate and are amenable to both laboratory and field-based studies. Despite the suitability of cichlids for studying the interactions between hormones and social status, most studies have concentrated on only a few representative African (e.g., *Astatotilapia burtoni, Oreochromis mossambicus, Oreochromis niloticus, Neolamprologus* spp.) and Neotropical [e.g., *Cichlasoma dimerus, Cichlasoma nigrofasciatus* (=*Amatitlania nigrofasciata*)] species (See Fig. 1 for summary of relevant characteristics).

Our goal for this review is to summarize some of the existing information on the endocrine and neuroendocrine molecules associated with male social status in one of the best studied African cichlid species, *Astatotilapia burtoni* [for reviews, see (Fernald and Maruska, 2012; Maruska and Fernald, 2014; Maruska and Fernald, 2018)]. We use *A. burtoni* as a case study but also make comparisons to other cichlids when relevant. Further, we focus on males because while females of several cichlids, including *A. burtoni,* may have social hierarchies under certain conditions, less is known about relationships between status and
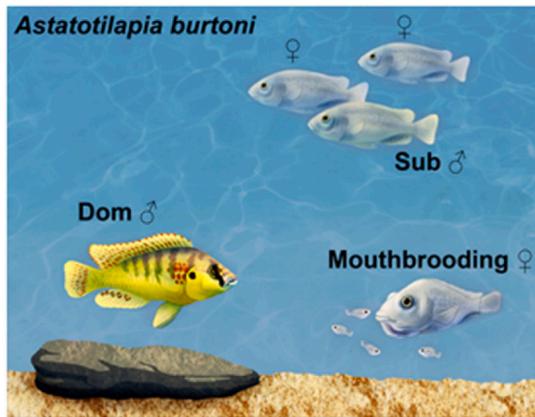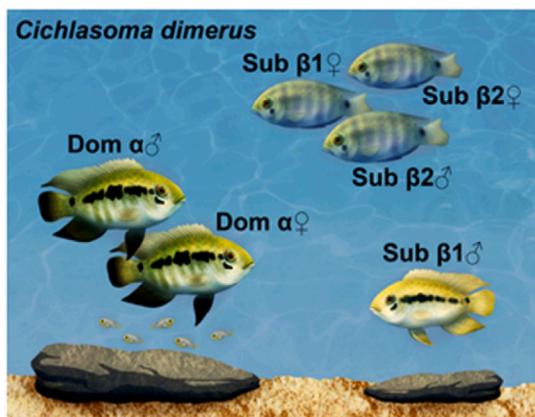
Fig. 1. Summary of dominance hierarchies, breeding, and parental care strategies in commonly studied cichlid species. The African *Oreochromis niloticus* and *O. mossambicus* have characteristics similar to *A. burtoni*, and the Central American convict cichlid (*Amatitlania nigrofasciata*) has characteristics similar to *C. dimerus*. Dom, dominant; Sub, subordinate; ♂, male; ♀, female.

hormones in females (Renn et al., 2012) (but see short section on females below). We discuss circulating hormones as well as endocrine and neuroendocrine signaling molecules acting in the brain or other tissues that fluctuate with social rank. One important caveat is that most studies describe differences in some physiological measure between dominant and subordinate individuals, but in many cases, it is unclear whether that measure is a result of the individual's social rank or the cause of it, which is important to consider. Further, it is also vital to recognize that most individual males within cichlid hierarchies are not just 'dominant' or 'subordinate' but rather, fall along a spectrum in which some males around them have a higher rank and others a lower rank. While the term dominance "status" often refers to dyadic situations and "rank" refers to a position in the hierarchy that depends on group composition, these terms and others (e.g., "state", "position") are used interchangeably here, as they are in the literature.

In the sections below, we summarize the relationships between social status and the hypothalamic-pituitary-gonadal (HPG) axis, circulating sex-steroids, hypothalamic-pituitary-interrenal (HPI) axis, other signaling molecules (e.g., nonapeptides, monoamines), and the influence of hormones on communication abilities associated with social rank. We also highlight that establishment and maintenance of a dominance hierarchy involves complex interactions among group members in which each individual must gather and translate sensory inputs and experience into a distinct, status-specific and integrated phenotype. Finally, we propose several areas of future research towards uncovering the mechanisms that underlie the role of hormones in establishing and maintaining social rank in cichlids. This work will provide important comparative insights for revealing conserved traits across vertebrates that contribute to the evolution of dominance hierarchies.

1.2. Social status and the HPG axis

Reproduction in all vertebrates is controlled by the conserved HPG axis, and the activity of this axis is tightly linked to social rank in many cichlid species (Maruska, 2014; Scaia et al., 2020). Because of this, it is difficult to separate the role of hormones in dominance specifically from the roles in reproductive behavior and physiology. In many cases, there are distinct profiles of HPG axis measures associated with dominant and subordinate social rank, but it is often not known whether they are the cause of or are the result of that rank. However, by examining males at different time points as they transition between social states (i.e., rising or falling in rank) we can provide some insights. With this caveat in mind, and the fact that the relationships between the HPG axis and social rank in cichlids were previously reviewed [e.g., (Maruska, 2014; Maruska and Fernald, 2014; Scaia et al., 2020)], we briefly summarize existing knowledge on HPG-related hormones during status transitions.

Studies across cichlids suggest that the initial expression of dominance is controlled centrally (i.e., by the brain) and independent of the gonadal endocrine system, which is supported by the observation that castrated male *A. burtoni* still perform dominance behaviors (Soma et al., 1996). Then, either sequentially or simultaneously to the expression of dominance behaviors, the HPG axis is stimulated to reinforce and maintain the dominant state and increase reproductive potential. Importantly, in *A. burtoni*, subordinate males maintain some level of HPG axis activity, including sperm production (Kustan et al., 2012; Maruska and Fernald, 2011), which facilitates the quick rise in rank. Similarly, during social descent and territory loss, males quickly fade their body coloration, adopt more submissive behaviors, and show elevations in serum cortisol levels (Maruska et al., 2013a), but changes along the HPG axis occur more slowly over days suggesting some 'defense' against loss of status (Parikh et al., 2006a; White et al., 2002). This is advantageous because males that are evicted from their territory may also immediately challenge another territory-holding male and quickly gain a new territory without having to completely descend to subordinate status. Interestingly, studies using immediate early genes as

proxies for neural activation demonstrate differential activation of brain regions involved in social decisions and stress coping between males rising and those falling in rank (Maruska et al., 2013a; Maruska et al., 2013b). This suggests that similar neural circuitry underlies expression of social state and that inputs from external sensory signals and internal physiological state are integrated in the brain to control social dominance and ultimately the reproductive axis. Thus, quick recognition and the decision to either rise or descend in rank results in modulation of the HPG axis to support the male's new position in the dominance hierarchy.

Reproduction in cichlids is controlled by gonadotropin-releasing hormone 1 (GnRH1) neurons in the hypothalamic preoptic area (Fig. 2) that project directly to the pituitary gland and stimulate production and release of the gonadotropin hormones (luteinizing hormone, LH; follicle stimulating hormone, FSH) to the bloodstream. Circulating LH and FSH bind to G-protein coupled receptors in the testes to promote spermatogenesis, and steroid synthesis and release. This HPG axis in *A. burtoni* is under social control, with distinct characteristics at every level (brain, pituitary, blood, testes) in dominant and subordinate males that rapidly change as they transition between social ranks [see (Maruska, 2014, 2015; Maruska and Fernald, 2014; Maruska and Fernald, 2018) for reviews] (Fig. 3). For example, when given an opportunity to gain a territory, a subordinate male will intensify his body coloration and eye-bar and begin performing aggressive and reproductive dominance behaviors within minutes (Burmeister et al., 2005; Maruska and Fernald, 2010a). GnRH1 neurons rapidly synthesize more decapeptide, increase their soma size, increase their dendritic complexity, and show pulsatile firing patterns to activate the reproductive axis [reviewed in (Fernald and Maruska, 2012; Maruska and Fernald, 2013, 2018)]. Similar upregulation is measurable in the pituitary (e.g. GnRH receptors, steroid receptors, gonadotropins), bloodstream (e.g. LH, FSH, sex-steroids), and testes (e.g. gonadotropin receptors, steroid receptors, gonadosomatic index, spermatogenesis) within minutes to hours to ramp up the reproductive system [reviewed in (Maruska, 2014; Maruska and Fernald, 2014; Maruska and Fernald, 2018)] (Fig. 3). The cellular and molecular mechanisms responsible for these changes require further study, but the protein kinase mechanistic target of rapamycin (mTOR) seems to play a role from the brain to the testes (Maruska et al., 2019).

Many of these same associations between social rank and HPG axis also occur in other African and Neotropical cichlids with similar and different mating systems (Alonso et al., 2012; Chee et al., 2013; Pfennig et al., 2012; Scaia et al., 2020). Thus, during social ascent, changes occur on the time scale of minutes to days after recognition of the opportunity indicating that they are a consequence of the social transition rather than the cause of it. It is likely that sensory and perceptual inputs of the opportunity first signal to decision, motivational, and motor regions of the brain to initiate dominance behaviors that secure territory ownership. Once ownership is established and the male looks and behaves like a dominant territory holder, subsequent physiological and morphological changes can occur to support and maintain the new status.

1.3. Social status and sex-steroids

Sex-steroid hormones (androgens, estrogens, and progestins) mediate several phenotypic traits that affect an organism's social standing. In *A. burtoni* and other cichlids, position in the social hierarchy is associated with variation in these hormones (Table 1) but seems to be a result of rather than a cause of rank, as mentioned above for the HPG axis (Maruska, 2014). When social status is experimentally manipulated up or down, changes in the circulating levels of hormones (released from cells into the bloodstream where they can potentially exert effects on many target tissues throughout the body) follow or are coincident with changes in the behavior and morphology that distinguish dominant and subordinate individuals (Maruska and Fernald, 2010a, 2013; Parikh et al., 2006b). Thus, there are multiple aspects of sex-steroid hormone biology that typify an individual's rank in the hierarchy and can
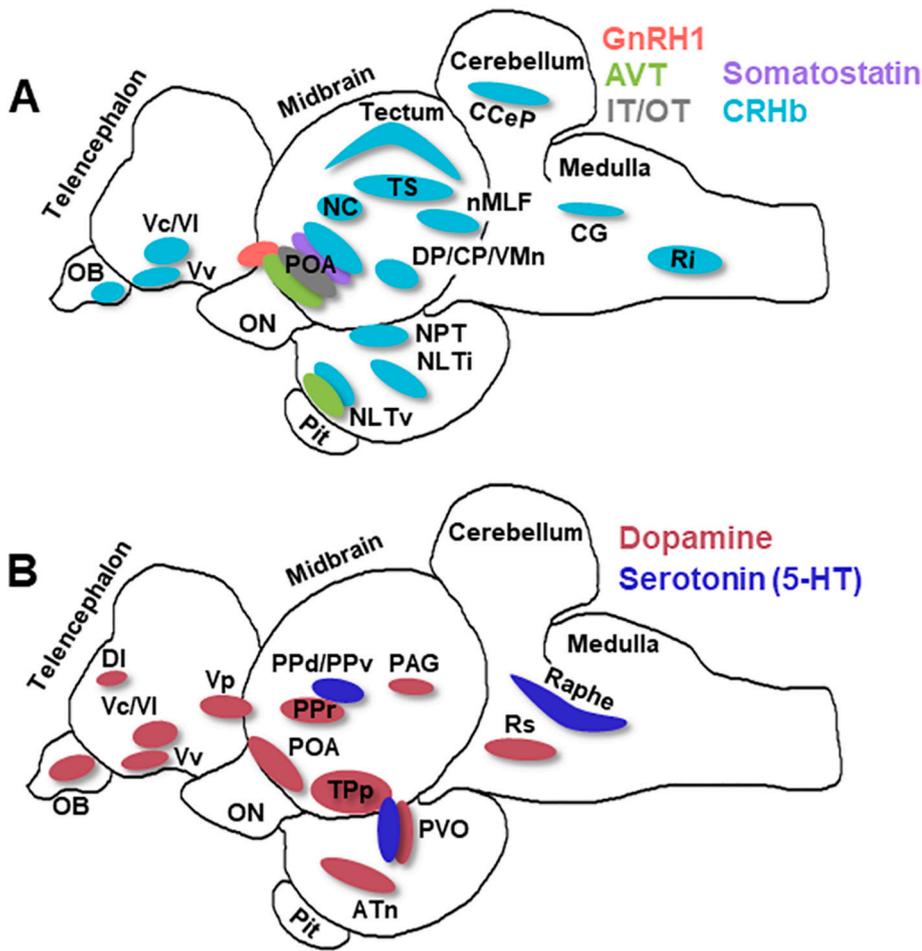
Fig. 2. Schematic sagittal diagrams of the *A. burtoni* brain to illustrate the locations of neuropeptide and monoamine cell populations associated with differences in male social rank. A) Gonadotropin-releasing hormone 1 (GnRH1), arginine vasotocin (AVT), isotocin/oxytocin (IT/OT), somatostatin, and corticotropin-releasing hormone b (CRHb) neurons are all localized to various nuclei of the preoptic area (POA). A small population of AVT neurons is also found in the ventral region of the lateral tuberal nucleus (NLTv), and both somatostatin and CRHb neurons are also found in other nuclei throughout the brain. B) Serotonin neurons are found in the PPv/PPd, preoptic area, paraventricular organ (PVO), and Raphe nuclei. Dopaminergic neurons labeled with an antibody against the rate-limiting enzyme tyrosine hydroxylase, are distributed in many regions throughout the brain. Locations of nuclei are only approximate, may be offset for visualization purposes, and some smaller populations of somata for CRHb, dopamine, and somatostatin are not shown. See the following references for more details on distribution patterns: [GnRH1, (Davis and Fernald, 1990); AVT, (Butler et al., 2021; Greenwood et al., 2008); IT/OT, (K.P. Maruska, unpublished results); Somatostatin, (Hofmann and Fernald, 2000)-reference also mentions cells in the ventrolateral telencephalon, tectum, caudal hypothalamus, medulla oblongata, and other areas, but exact locations were not reported so they are not shown here; CRHb, (Grone et al., 2021); Serotonin, (Loveland et al., 2014); Dopamine, (O'Connell et al., 2011)]. Abbreviations: ATn, anterior tuberal nucleus; CCeP, purkinje layer of corpus cerebellum; CG, central gray; CP, central posterior thalamic nucleus; Dl, lateral zone of the dorsal telencephalon; DP, dorsal posterior thalamic nucleus; NC, nucleus corticalis; NLTi/NLTv, intermediate and ventral parts of lateral tuberal nucleus; nMLF, nucleus of the medial longitudinal fasciculus; NPT, posterior tuberal nucleus; OB, olfactory bulb; ON, optic nerve; PAG, periaqueductal gray; Pit, pituitary; POA, preoptic area; PPd/PPv/PPr, dorsal, ventral, and rostra periventricular pretectal nucleus; PVO, paraventricular organ; Ri/Rs, inferior and superior reticular formation nucleus; TPp, periventricular nucleus of the posterior tuberculum; TS, torus semicircularis; Vc, central part of the ventral telencephalon; Vl, lateral part of the ventral telencephalon; VMn, ventromedial thalamic nucleus; Vp, postcommissural nucleus of the ventral telencephalon; Vv, ventral part of the ventral telencephalon.

ultimately help regulate physiological changes at many levels to support their social position.

In teleosts, the major androgens are testosterone (T) and 11-ketostestosterone (11-KT, a fish-specific potent androgen), and levels of T and 11-KT are often positively correlated with each other within an individual species. In many cichlids, dominant or territorial males have higher circulating androgens compared to subordinate males [tilapia *O. mossambicus* (Golan and Levavi-Sivan, 2013; Oliveira et al., 1996) and *O. niloticus* (Pfennig et al., 2012), *C. dimerus* (Ramallo et al., 2015), *P. nyererei* (Dijkstra et al., 2007), *N. pulcher* (Taves et al., 2009), *A. burtoni* (Huffman et al., 2012; Maruska, 2015; Maruska and Fernald, 2010c; Parikh et al., 2006b)] (see Table 1). Intramuscular injections of T into male *A. burtoni* affects both reproductive and aggressive behaviors (Fernald, 1976). Similarly, aggression towards other males and reproductive effort towards females are positively correlated with circulating androgens (Huffman et al., 2012; Maruska, 2015). Circulating levels of T also correlate with total male-directed aggression towards an intruder in a dominant male's territory, and T co-varies with aggression and expression of several important neuromodulatory receptors in the medial part of the dorsal telencephalon (Weitekamp and Hofmann, 2017). Castrated male *A. burtoni* have reduced androgen levels and aggression, but larger GnRH1 neurons in the POA than sham-operated

fish (Francis et al., 1993; Soma et al., 1996). This hypertrophy of GnRH1 cells by castration can be reversed by treatment with androgens, yet dominant males with higher circulating androgens have larger GnRH1 somata, suggesting that the larger GnRH1 cells of dominant males are not due to gonadal hormones (Francis et al., 1992). Castration in another cichlid (*O. mossambicus*), however, had no effect on aggression but eliminated nest building and courtship behaviors (Almeida et al., 2014), suggesting both species-specific and behavior-specific androgen effects in cichlids.

Circulating levels of androgens are also influenced by other factors, even within a social status, which can ultimately influence the structure and stability of the dominance hierarchy. For example, circulating androgens are higher in *A. burtoni* and male convict cichlids during social (both reproductive and competitive) compared to non-social contexts (Sessa et al., 2013; Weitekamp et al., 2017a), highlighting androgen importance in all behaviors important for hierarchy maintenance. Testosterone is also related to social network stability in *A. burtoni* where more stable networks were associated with greater T differences between dominant and subordinate males while more unstable communities showed similar T levels between social ranks (Maguire et al., 2021). Further, increases in androgens, especially 11-KT, after male-male contests are consistent with the challenge hypothesis (e.g.,
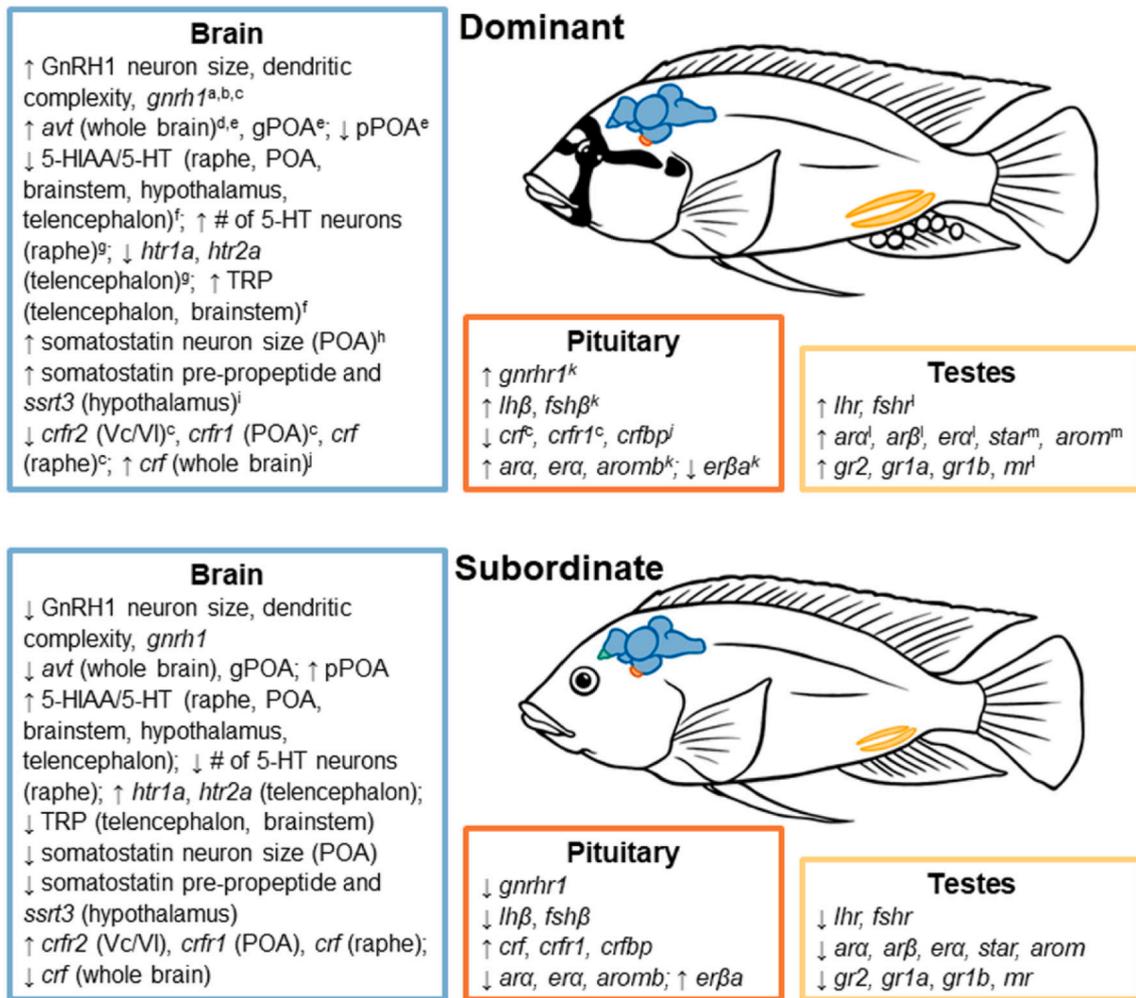
Fig. 3. Summary of differences in endocrine and neuroendocrine signaling molecules between dominant and subordinate *A. burtoni* males in the brain, pituitary, and testes. ↑, greater relative levels; ↓, lower relative levels. Components of steroid signaling (enzymes, receptors) in the brain are not included here because differences vary widely by brain region analyzed [see the following references and those cited in the text: (Burmeister et al., 2007; Huffman et al., 2013; Maruska et al., 2013b; Renn et al., 2008)]. Abbreviations: 5-HIAA, 5-hydroxyindoleacetic acid; 5-HT, 5-hydroxytryptomine or serotonin; *arα/arβ*, androgen receptor α/β; *arom*, aromatase; *avt*, arginine vasotocin; *crf*, corticotropin releasing factor; *crfr1/crfr1*, crf receptor 1/2; *crfbp*, crf binding protein; *erα/erβ*, estrogen receptor α/βa; *fshβ*, follicle stimulating hormone β; *fshr*, fsh receptor; *gnrh1*, gonadotropin releasing hormone 1; *gnrhr1*, gnrh receptor 1; gPOA, gigantocellular POA; *gr1a/gr1b/g2*, glucocorticoid receptor 1a/1b/2; *htr1a/htr2a*, serotonin receptor 1a/2a; *lhβ*, luteinizing hormone β; *lhr*, lh receptor; *mr*, mineralcorticoid receptor; POA, preoptic area; pPOA, parvocellular POA; *ssrt3*, somatostatin receptor 3; *star*, steroidogenic acute regulatory protein; TRP, tryptophan; Vc/Vl, central and lateral parts of the ventral telencephalon. References are shown on dominant male values but are identical for subordinates: [a](Davis and Fernald, 1990), [b](Maruska and Fernald, 2013), [c](Carpenter et al., 2014), [d](Renn et al., 2008), [e](Greenwood et al., 2008); [f](Winberg et al., 1997); [g](Loveland et al., 2014); [h](Hofmann and Fernald, 2000); [i](Trainor and Hofmann, 2006); [j](Chen and Fernald, 2008); [k](Maruska et al., 2011); [l](Maruska and Fernald, 2011); [m](Huffman et al., 2012).

androgens increase to promote aggression during mating in seasonal breeders) across multiple cichlid species (e.g., *N. pulcher, Lamprologus callipterus, Tropheus moori, Pseudosimochromis curvifrons, O. mossambicus, A. burtoni*) (Desjardins et al., 2006; Hirschenhauser and Oliveira, 2006; Hirschenhauser et al., 2004; Maruska and Fernald, 2010a). Androgen levels may also vary among individuals that hold the same social status. In *A. burtoni*, for example, males of both dominant and subordinate status display one of two color phenotypes, blue and yellow. Dominant yellow males, which are more aggressive than dominant blue males, have higher circulating 11-KT levels compared to dominant blue morphs, but T levels do not differ (Dijkstra et al., 2017; Korzan et al., 2008). Further, subordinate yellow males have higher androgen levels when forced to confront dominant blue males compared to when they encounter dominant yellow males (Korzan et al., 2008). Collectively these studies highlight the complexity of androgen signaling that may be species-specific, and how fluctuations in circulating androgens can be influenced not only by an individual males' internal state and social position, but also by the types of social interactions they encounter within the population.

Estrogens and progestins are also influenced by changes in male social status but are less studied compared to androgens (see Table 1). In *A. burtoni* males, circulating levels of 17β-estradiol and progestins are higher in dominants than subordinates (Maruska, 2015; Maruska and Fernald, 2010c; O'Connell et al., 2013a). Socially ascending males show increases in serum estradiol and progestins within 30 min., with further increases seen in more established dominant males (Maruska, 2015). Progestins and estradiol are positively correlated with reproductive behaviors in *A. burtoni* males, like androgens (Maruska, 2015). Male *A. burtoni* also increase their courtship efforts in the presence of 17α,20β-progesterone (17α,20β-P), a potential pheromone for this species (Kidd et al., 2013). Estrogens modulate aggressive behaviors in *A. burtoni* independent of social status (O'Connell and Hofmann, 2012), and levels are positively correlated with some aggressive and most reproductive behaviors (Maruska, 2015). In another study that characterized two subclasses of dominant males, males establishing a territory showed escalating aggression and courtship and had higher levels of estradiol

Table 1
Summary of differences in circulating steroid hormone levels in dominant (D) and subordinate (S) male cichlids.

Hormone	Species	Direction of difference	Citations
Testosterone	Astatotilapia burtoni	D > S	(Huffman et al., 2012; Korzan et al., 2014; Maguire et al., 2021; Maruska, 2015; Maruska and Fernald, 2010c; Maruska et al., 2012; Maruska et al., 2013b; O'Connell et al., 2013a; Parikh et al., 2006b)
	Oreochromis mossambicus	D > S	(Oliveira et al., 1996)
	Neolamprologus pulcher	D > S	(Aubin-Horth et al., 2007)
	Cichlasoma dimerus	D > S	(Ramallo et al., 2015)
11-ketotestosterone	Astatotilapia burtoni	D > S	(Korzan et al., 2014; Loveland et al., 2014; Maruska, 2015; Maruska and Fernald, 2010c; Maruska et al., 2012; Maruska et al., 2013b; Parikh et al., 2006b)
	Oreochromis mossambicus	D > S	(Oliveira et al., 1996)
	Oreochromis niloticus	D > S	(Golan and Levavi-Sivan, 2013; Pfennig et al., 2012)
	Neolamprologus pulcher	D > S	(Taves et al., 2009)
	Cichlasoma dimerus	D > S	(Morandini et al., 2014; Ramallo et al., 2015)
	Pundamilia nyererei	D > S	(Dijkstra et al., 2007)
Estradiol	Astatotilapia burtoni	D > S	(Maruska, 2015; Maruska et al., 2012; Maruska et al., 2013b; O'Connell et al., 2013a)
	Cichlasoma dimerus	D < S	(Ramallo et al., 2015)
Progesterone/ Progestins	Astatotilapia burtoni	D > S	(Maruska, 2015)
	Oreochromis mossambicus	D > S	(Oliveira et al., 1996)
Cortisol	Astatotilapia burtoni	D > S	(Maruska et al., 2013b)
		D < S	(Carpenter et al., 2014; Fox et al., 1997; Korzan et al., 2014; Maguire et al., 2021)
	Oreochromis niloticus	D < S	(Alonso et al., 2011; Alonso et al., 2012)
	Neolamprologus pulcher	D > S	(Buchner et al., 2004; Mileva et al., 2009)
		D < S	(Culbert et al., 2018)
	Cichlasoma dimerus	D < S	(Alonso et al., 2012; Morandini et al., 2014; Ramallo et al., 2015)

>, greater than; <, less than. Studies where no statistical differences were observed are not included.

(and androgens) compared to males with established territories that had more stable aggression and courtship (Alcazar et al., 2016). Therefore, higher serum sex-steroids are most often associated with males of higher status, especially those performing more aggressive and reproductive behaviors. In contrast however, non-territorial *C. dimerus* males have higher circulating estradiol levels compared to territorial males, suggesting the relationships differ among species (Ramallo et al., 2015). Thus, like androgens, estradiol and progestins appear to be involved in both reproductive and aggressive behaviors associated with dominance. Collectively, these studies suggest important relationships between behavioral repertoire and levels of all circulating sex-steroids, but because steroids can fluctuate rapidly, it is also important to recognize that different experimental paradigms can show variations in steroid responses and their functional interpretations.

1.3.1. Enzymes involved in sex-steroid synthesis

Aromatase, the enzyme that converts T to estradiol, and steroidogenic acute regulatory protein (StAR), the rate-limiting enzyme of T synthesis are both potentially involved in sex-steroid influence of dominance (Fig. 3). StAR levels in the testes rise in *A. burtoni* in the transition from subordinate to dominant status, which is coincident with increased sex-steroid levels and testis maturation (Huffman et al., 2012). Expression of gonadal aromatase (CYP19) also fluctuates in the testes during status transitions, with a trend towards higher levels in males transitioning to dominance status, but this was not always statistically significant (Huffman et al., 2012; Maruska and Fernald, 2011). In the brain, levels of aromatase are higher in whole brains of dominant compared to subordinate males (Renn et al., 2008), and differ among subordinate, ascending, and dominant males in specific micro-dissected nuclei that suggests estrogenic regulation of specific neural circuits (Maruska et al., 2013b). Further, dominant males express more aromatase than subordinates in the olfactory bulbs (Maruska and Fernald, 2010b), but subordinate males have greater expression of aromatase in the gigantocellular and magnocellular regions of the preoptic area (POA) (Huffman et al., 2013) suggesting that regional brain differences within each social status are important for function. Inhibiting

aromatase with fadrozole also results in reduced aggression by dominant males, although reproductive output is maintained (Huffman et al., 2013). These studies primarily suggest higher sex-steroid synthesis in the brain and testes of males in higher social positions. However, it is likely that local sex-steroid production in specific neural circuits of the brain is the main regulator of behaviors associated with social rank, while peripheral steroid synthesis may contribute to other physiological processes associated with dominance or maintaining the current social position until a change in rank occurs.

1.3.2. Sex-steroid receptors

The sites of action and relative sensitivity of the brain and other tissues to sex-steroids depends on the localization and abundance of their receptors. *A. burtoni* has three estrogen (ERα, ERβa, ERβb), one progesterone (PGR), and two androgen (ARα, ARβ) receptors that are nuclear transcription factors (membrane estradiol receptor, GPER1 is also present, but not yet studied in the dominance context) (Burmeister et al., 2007; Butler et al., 2019; O'Connell and Hofmann, 2012). In the testes, levels of *erα* mRNA increase within hours of social ascent and are higher in dominant compared to subordinate males (Maruska and Fernald, 2011). In contrast, levels of *erβa* and *erβb* are elevated several days after rising in rank, but do not differ between stable dominant and subordinate males (Maruska and Fernald, 2011). The two different androgen receptors in *A. burtoni* seem to play different roles in the reproductive biology of dominant males (Alward et al., 2020), and their expression levels also change in the testes with male social status. For example, mRNA levels of *arα* and *arβ* are higher in the testes of dominant compared to subordinate males but fluctuate up and down during social ascent (Maruska and Fernald, 2011) (but see Burmeister et al., 2007 that did not find status differences). Thus, the testes appear to be more sensitive to estradiol and androgen feedback as testes grow and increase sex-steroid synthesis, possibly to support maintenance of spermatogenesis in the reproductively active dominant males. CRISPR/Cas9 editing of *A. burtoni* ARs also shows that ARβ, but not ARα, is necessary for testes growth (Alward et al., 2020). Nothing is known, however, about the relationship between dominance and expression levels of PGR in the

testes of *A. burtoni* or other cichlids.

Sex-steroid receptor subtypes also differ in the brain with male social rank, and manipulations with antagonists and agonists can affect aggressive and reproductive behaviors. For example, estrogen receptor subtypes show differential mRNA expression in several micro-dissected nuclei among subordinate, ascending, and dominant *A. burtoni* males (Maruska et al., 2013b), and in larger macro-dissected brain regions (e. g. anterior brain) between dominant and subordinates (Burmeister et al., 2007). However, other studies using in situ hybridization did not find status differences in ERs in some of these same regions (O'Connell et al., 2013a), highlighting the variability in interpretations based on methodological variations. Experimental manipulation of estrogens also modulates aggression in both dominant and subordinate *A. burtoni* males (O'Connell and Hofmann, 2012), and both antagonists and agonists of ERs increase reproductive-associated digging in convict cichlids (Sessa et al., 2013). Levels of PGR were examined in several social brain regions but did not show differences between dominant and subordinate *A. burtoni* males (O'Connell et al., 2013a), and manipulation of PGR modifies courtship behavior only in dominant males (O'Connell and Hofmann, 2012). Early life circumstances may also mediate endocrine biology later in life: group rearing of *A. burtoni* in early life results in fish with greater expression of estrogen (and androgen) receptors in the brain than fish raised in pairs (Solomon-Lane and Hofmann, 2019). Estradiol signaling may be involved in multiple dominance behaviors in male cichlids, while progesterone signaling may be more restricted to reproduction, but this requires further study.

Androgen receptor subtypes are also differentially expressed in the brain when examined at both macro- and micro-dissected scales (Burmeister et al., 2007; Harbott et al., 2007; Maruska et al., 2013b). In most cases, levels of both *arα* and *arβ* are higher in either ascending or dominant males compared to subordinate males, suggesting that the brain shows increased androgen sensitivity as males attain higher ranking status. Further, manipulations of AR in *A. burtoni* modify only courtship behaviors in dominant males (O'Connell and Hofmann, 2012). When provided an opportunity to rise in rank, socially ascending males are more likely than dominant males to show sequential aggressive displays, and antagonism of ARs via injection with cyproterone acetate increases the time between these successive behaviors (Alward et al., 2019). In the convict cichlid *Amatitliana nigrofasciata*, AR antagonists increase approaches towards females and reduce aggression towards males, while AR agonists increase digging, a part of the male reproductive repertoire that prepares the territory for spawning (Sessa et al., 2013). Thus, there is evidence that androgens interacting with their receptors in the brain can influence many of the dominance-related behaviors across cichlid species. The exact mechanisms, however, will require further investigation to reveal any commonalities or species-specific adaptations across cichlids.

1.4. Social status and the HPI axis

The hypothalamic-pituitary-interrenal (HPI; analogous to hypothalamic-pituitary-adrenal, HPA) axis is activated in response to stressors, which can be anything that causes a state of physical, emotional, or psychological strain in an organism. The HPI/HPA axis is a major neuroendocrine system that controls reactions to stress and regulates many body processes, including the immune system, mood and emotions, reproduction, energy storage and expenditure, and others. Across taxa, both rises and falls in social rank often activate the HPI/HPA axis which results in the release of glucocorticoids (e.g., steroids such as cortisol, corticosterone) to the bloodstream (Creel, 2001; Sapolsky, 2005). In the context of dominance, these glucocorticoids may lead to metabolic, physiological, and behavioral changes to help individuals deal with the stressors associated with their position in the hierarchy.

In fishes, cortisol release is controlled by corticotropin-releasing hormone (CRH; also called corticotropin-releasing factor, CRF; terms are used interchangeably below as originally reported in different studies) neurons in the brain, which cause release of adrenocorticotropic hormone (ACTH) from the pituitary gland into circulation to reach the interrenal tissue (located in head kidney, which is analogous to the adrenal glands in mammals and birds) where cortisol is synthesized. Because both gain and loss of a particular social rank can be stressful, requiring mobilization of energetic resources, and activation of the stress axis often has inhibitory effects on the HPG axis across vertebrates (Nikolarakis et al., 1986; Rivier and Rivest, 1991), several studies examined the role of the HPI axis on dominance and social rank in *A. burtoni* and other cichlids. Below we summarize the relationships between an individual's social rank and HPI axis activity from the brain to the release of cortisol into the circulation, with comments on potential functions related to dominance.

At the apex of the HPI axis in cichlids, neurons expressing *crhb* (along with other members of this peptide family, *urotensin 1*, *urocortin 2 and 3*) are widely distributed in the brain of *A. burtoni* (Fig. 2), suggesting multiple functions for this family of neuropeptides related to social status (Grone et al., 2021). For example, dominant male *A. burtoni* have higher levels of *crhb* mRNA in the whole brain, greater *crf receptor 1* (*crfr1*) mRNA in the pituitary, and lower *crf binding protein* (*crfbp*) mRNA in the pituitary compared to subordinate males (Chen and Fernald, 2008) (Fig. 3). Authors suggest that high cortisol in subordinates down-regulates brain CRF signaling as a homeostatic mechanism under long-term stress. In a subsequent study examining the CRH signaling system with higher neuroanatomical resolution in the brain, differences occurred between dominant and subordinate males, as well as rapid changes within 15 min of social ascent. For example, *crf* and *crfr1* mRNA levels are lower in the pituitary of ascending males compared to stable subordinate males suggesting down-regulation during a rise in status (Carpenter et al., 2014). In the central and lateral nuclei of the ventral telencephalon (Vc/Vl) where CRH cell bodies are abundant, *crfr1* and *crfr2* mRNA is lower in ascending males compared to stable subordinate males. In the POA, where GnRH1 neurons are located, ascending and stable dominant males have lower levels of *crfr1* expression compared to subordinate males. This work suggests that elevated CRH and cortisol signaling in socially subordinate animals may serve as a coping-strategy to maintain reduced reproductive and aggressive activity while living with larger, dominant conspecifics. Visual signals from dominant males alone do not result in this long term CRH and cortisol signaling elevation (Chen and Fernald, 2011); thus, other sensory signals such as urine released from dominant males may be necessary to trigger the elevated stress response that is characteristic of subordinate males.

Because the CRH signaling system often exerts an inhibitory effect on the reproductive axis, rapidly decreasing CRH signaling in the brain and pituitary upon social ascent may disinhibit the HPG axis during a rise in social rank (Carpenter et al., 2014). This removal of the inhibitory central CRH system may facilitate the physiological changes, especially in POA GnRH1 cells, that these ascending fish require to rapidly achieve reproductive viability as they rise in rank and acquire a breeding territory. The GnRH1 gene also contains regulatory regions for glucocorticoid receptors (White and Fernald, 1998), and there are differences between dominant and subordinate males in levels of certain glucocorticoid receptors in the POA (Korzan et al., 2014), suggesting the HPG axis is influenced by HPI axis signaling. It is also likely that CRH signaling is important during social descent, but this remains to be investigated in *A. burtoni*. In *A. burtoni* and other fishes, *crf*, *crf receptors*, and *crfbp* mRNA are also found in peripheral tissues including the retina, gills, skin, spleen, kidney, intestine, ovary, testis and others (Chen and Fernald, 2008; Grone et al., 2021; Grone and Maruska, 2015), but whether these sources play a role in dominance or social rank are not clear.

The next level of the HPI axis is release of ACTH from the pituitary gland, but how this hormone is impacted by male social status is not known in *A. burtoni* or other cichlids and deserves future attention. The downstream effect of HPI axis activation is release of cortisol into the

bloodstream, where it can exert effects on any tissue that expresses glucocorticoid receptors. In the context of social rank in cichlids, both subordinate and dominant males deal with different types of stressors, making relationships between cortisol and social status complicated (see Table 1). Circulating cortisol levels can change rapidly and are often reflective of fish experience during the minutes prior to sampling such that variations in social composition, hierarchy stability, fish density, male color morph, and experimental paradigms report conflicting cortisol measures associated with male *A. burtoni* rank (Carpenter et al., 2014; Fox et al., 1997; Korzan and Fernald, 2007; Korzan et al., 2008). For example, studies report higher plasma cortisol levels in subordinate compared to dominant males (Carpenter et al., 2014; Fox et al., 1997; Maguire et al., 2021), higher levels in dominant compared to subordinate (Maruska et al., 2013b), or no differences between social states (Maruska, 2015; Maruska and Fernald, 2010c). Along with dramatic color changes and displays of different behaviors, both ascending and descending *A. burtoni* males show rapid increases in plasma cortisol levels (Fox et al., 1997; Maruska et al., 2013a; Maruska et al., 2013b; Parikh et al., 2006a). Cortisol can help direct metabolic energy away from costly long-term physiological processes to focus on dealing with an immediate stressor (McEwen and Seeman, 1999). Thus, rapid increases in cortisol during status transitions likely function to help allocate resources in support of the physiological needs required for the individual's new social position. In subordinate male *A. burtoni,* suppression of the entire reproductive axis occurs, and along with higher cortisol levels, these males have lower plasma levels of gonadotropins and sex-steroid hormones (Maruska, 2015; Maruska et al., 2011), smaller GnRH1 neurons (Davis and Fernald, 1990), and smaller testes (Maruska and Fernald, 2011). In the testes, however, subordinate males have low mRNA levels of glucocorticoid receptors (*gr1a, gr1b, gr2*) and mineralocorticoid receptor, all of which bind cortisol, suggesting more of a homeostatic mechanism at the testes (e.g., high cortisol in subordinates down-regulates testes receptor levels as part of negative feedback) (Greenwood et al., 2003; Maruska and Fernald, 2011). Ultimately, by diverting energy away from reproduction, subordinate males can invest more in somatic growth that provides an advantage when acquiring a vacant territory or challenging a current territory-holding male (Hofmann et al., 1999). The differences in the *A. burtoni* HPI axis observed in the brain, pituitary, and testes associated with male rank indicate important but complicated roles in regulating social status, particularly in the trade-offs with reproduction, but exact mechanisms are not yet clear.

The role of the HPI axis in social dominance hierarchies appears equally complicated in other cichlids, but again, may be in part due to differences in experimental design across studies. In the group living African cichlid fish *N. pulcher*, for example, levels of cortisol and transcripts of glucocorticoid receptors *gr1* and *gr2* in the POA are higher in socially ascending males compared to dominant males (Culbert et al., 2018). Further, transcripts of *star* and cytochrome *p450* side-chain cleavage enzyme (*p450scc*) that are involved in cortisol synthesis are upregulated in the head kidney of ascending compared to dominant males, indicating greater cortisol production in socially ascending fish (Culbert et al., 2018). However, as with *A. burtoni*, there is conflicting evidence on circulating cortisol levels in dominant and subordinate *N. pulcher*, with one study reporting elevated cortisol in subordinates (Culbert et al., 2018) and another reporting elevated cortisol levels in dominants (Buchner et al., 2004). In the South American cichlid *C. dimerus*, dominant males and females have lower circulating cortisol levels than lower ranking individuals of the same sex (Alonso et al., 2011; Alonso et al., 2012). Further, subordinate *C. dimerus* males have larger steroidogenic interrenal cells, which produce cortisol, and these larger cells are correlated with higher levels of circulating cortisol (Morandini et al., 2014). In contrast, there is no difference in circulating cortisol levels in dominant and subordinate male Mozambique tilapia (*O. mossambicus*) (Almeida et al., 2012). These variations in cortisol measures among cichlid species also exist in other taxa, and the higher

circulating glucocorticoid levels observed in many experimental paradigms is often an acute effect that is not detected when comparing basal levels between social states in stable groups (Abbott et al., 2003; Creel, 2001). A meta-analysis of cortisol levels and dominance status in 25 bird and mammal species found that across species, dominant and subordinate individuals were equally as likely to have elevated basal glucocorticoid levels (Creel, 2001). This variation could be due to many factors such as aggressive and submissive behavioral differences among species, different mating and reproductive strategies, or disparate physiological mechanisms regulating the HPI/HPA axis. Future work characterizing cortisol and CRH signaling as a function of social status in a wider range of cichlid species will increase our understanding of the inter-specific variation associated with the HPI axis and social status. Further, the association of plasma androgen levels with status-seeking behavior depends on the level of cortisol in many species (e.g., dual hormone hypothesis) (Knight et al., 2020), so androgen x cortisol interactions also deserve more attention in cichlids.

1.5. Social status and other relevant signaling molecules

1.5.1. Serotonin (5-HT)

Serotonin is a ubiquitous monoamine transmitter shown to modulate aggressive and reproductive pathways in several cichlid species, especially submissive behaviors. In species like *A. burtoni* where dominance is tightly linked to reproductive ability, it is important to understand how the serotonergic system impacts behaviors leading to an upregulated reproductive axis. In vertebrates, the main populations of serotonergic neurons are found in the raphe nuclei of the hindbrain (Jacobs and Azmitia, 1992; Lillesaar, 2011), but in *A. burtoni*, additional neuronal populations are identified in the dorsal and ventral periventricular pretectal nuclei and the nucleus of the paraventricular organ (Loveland et al., 2014) (Fig. 2). Dominant males also have more 5-HT neurons in the raphe, with more drastic differences in the medial region, compared to subordinates (Loveland et al., 2014). Further, changes in the ratio of 5-hydroxyindolecacetic acid (5-HIAA), a serotonin metabolite, to 5-HT in the raphe and POA showed subordinate males had higher ratios than dominants. This ratio is often used as a measure of serotonin turnover, indicative of a larger serotonin demand in the brain (Bliss et al., 1972; Winberg et al., 1992), and shows that serotonin turnover in multiple brain regions was higher in subordinates. An earlier study also showed similar higher 5-HT turnover in the brainstem, telencephalon, and hypothalamus of subordinate males (Winberg et al., 1997) (Fig. 3). Further, activation of raphe neurons in *A. burtoni* is associated with displays of reactive stress coping behaviors (e.g., fleeing, hiding) following social defeat (Butler et al., 2018). Thus, 5-HT signaling in multiple brain regions likely contributes to maintaining physiological and behavioral aspects of social rank.

Differences in the expression of tryptophan (TRP), the serotonin precursor, also exist between dominant and subordinate *A. burtoni* males. For example, subordinate males have lower TRP levels in the telencephalon and brainstem that is accompanied by high 5-HT turnover, demonstrating that subordinate males maintain serotonergic activity despite low TRP availability (Winberg et al., 1997) (Fig. 3). Studies in other cichlid species explore the interaction between TRP and social dominance using dietary TRP. The cichlid fish, *C. dimerus*, was used to analyze how dietary TRP impacts 5-HT levels in the brain and conspecific agonistic interactions in males (Morandini et al., 2019). Male dyads in which both males received a TRP diet had longer latency to first attack and displayed more submissive behaviors (passive coping and retreat) than male dyads fed control diets. Although there were no significant interactions between dominance status and diet, subordinate males had higher 5-HIAA/5-HT ratios in the tectum, telencephalon, and POA/hypothalamus and higher 5-HIAA in the telencephalon, and POA/hypothalamus. Overall, these studies demonstrate the importance of the serotonergic system in mediating subordinate status in dominance hierarchies.

Several studies in cichlids have explored relationships among factors regulating activity of the serotonergic system and aggression. The cholesterol-serotonin hypothesis suggests low serum cholesterol leads to low serotonergic activity and increased aggressive behaviors (Kaplan et al., 1997; Kaplan et al., 1991). Nile tilapia (*O. niloticus*) treated with statin, a compound that lowers circulating cholesterol, display more aggressive behaviors during agonistic interactions, and have lower 5-HIAA expression and 5-HIAA/5-HT ratios in the telencephalon making this the first study in support of the cholesterol-serotonin hypothesis in non-mammalian vertebrates (Aguiar and Giaquinto, 2018). PL-*p*-Chlorophenylalanine (PCAP), a serotonin agonist, injected into male firemouth cichlids, *Thorichthys meeki,* increased aggressive behaviors (bites) compared to control males, supporting the idea that serotonergic activity mediates submissive behaviors (Adams et al., 1996). Intracranial injections of 5-HT also inhibited aggressive behavior in the Blue Acara cichlid, *Aequidens pulcher* (Munro, 1986). Although these studies emphasize the importance and role of serotonin in social dominance in cichlids, more studies are required to shed light on where in the brain serotonergic signaling functions to mediate submissive and dominance behaviors by focusing on the multitude of 5-HT receptor types. For example, in *A. burtoni*, expression levels of serotonin receptors *htr1a* and *htr2a* are higher in the telencephalon of subordinates, emphasizing their importance in mediating behavioral and physiological differences in social status (Loveland et al., 2014). Further, administration of 5-HT$_{1A}$ agonist increased aggression and decreased submission and affiliation in the cooperatively-breeding cichlid *N. pulcher*, while a receptor antagonist had opposite effects (Stettler et al., 2021). This suggests that this receptor type plays a role in both aggressive and socio-positive behaviors in this species, but also highlights the need to examine functions of different receptors throughout the brain in different species and contexts to truly understand the diverse roles 5-HT might play in regulating social rank.

1.5.2. Dopamine

Several studies have explored the role of dopamine (DA) in dominance and social hierarchies of cichlids. Dopamine is a neurotransmitter involved in modulating reproduction, aggressive behavior and physiology, is an important component of mesolimbic reward pathways, and can alter motivational states in different social contexts where decision making is crucial (Dufour et al., 2010; Macedo-Lima and Remage-Healey, 2021; Perelmuter et al., 2019). The distribution of DA cells and their receptors as part of the reward system is described in the brain of *A. burtoni* (Fig. 2), along with neurochemical profiling of different DA neuron groups (O'Connell et al., 2011, 2013b). DA activity in different brain regions, however, does not appear to differ between dominant and subordinate males (Winberg et al., 1997). Weitekamp et al. explored differences in aggressive behavior among *A. burtoni* males in the presence or absence of a reproductive opportunity (Weitekamp et al., 2017b). They found that males were more likely to display aggression towards an intruder in the presence of a gravid female and manipulating the expression of the D2 dopamine receptor using receptor agonists and antagonists reduced this aggressive behavior towards the male intruder in the same behavioral context. Further, a visual challenge (but not chemosensory stimuli) from dominant males activates DA neurons in a region of the ventral telencephalon of dominant males (O'Connell et al., 2013c). These studies demonstrate the importance of the DA system in mediating context dependent behavior in *A. burtoni*. Further, because dominance is directly linked to reproductive potential in many cichlids, studies have investigated the role of the DA system in regulating the activity of the HPG axis, where it is often inhibitory. For example, DA inhibits both basal and GnRH1-inhibited LH release from the pituitary in tilapia (Levavi-Sivan et al., 1995), hyperpolarizes GnRH1 neurons via action at D2-receptors in *A. burtoni* (Bryant et al., 2016)*,* and is involved in stress-induced suppression of reproduction in *O. mossambicus* (Chabbi and Ganesh, 2015). Because dopamine has links to reward, stress, decision, and reproductive circuitry in the brain, it seems likely that

dopaminergic signaling plays multiple and complex roles in regulating an individual's position in a dominance hierarchy.

1.5.3. Nonapeptides

Nonapeptides (peptide chains of 9 amino acids) such as arginine vasotocin (AVT; homologous to mammalian arginine vasopressin) and the lesser-studied isotocin (IT; homologous to mammalian oxytocin) are highly conserved molecules that collectively play a role in cardiovascular function, osmoregulation, stress, and social behavior across vertebrates (Balment et al., 2006; Bass and Grober, 2001; Godwin and Thompson, 2012; Goodson and Bass, 2001; Goodson et al., 2003). In teleosts, AVT and IT-synthesizing neurons are primarily found in the parvocellular, magnocellular, and gigantocellular regions of the POA (Fig. 2), a brain region heavily involved in sensory integration, decision-making, and many different social behaviors. While many studies in fishes show associations between nonapeptides and social status (Godwin and Thompson, 2012; Goodson and Bass, 2001), there is considerable variation among species, how nonapeptides are measured in different studies, and other variables that make generalizable functions difficult. Some of the key studies are summarized below.

Several studies explored the role of AVT in male *A. burtoni* social rank using different approaches. Intraperitoneal injections of AVT into stable dominant males makes them less aggressive and more likely to socially descend to a subordinate state (Huffman et al., 2015). Further, subordinate males in unstable hierarchies are less likely to socially ascend when injected with AVT, and AVT receptor antagonist decreases aggression and increases reproductive behaviors. Lastly, dominant males have higher whole brain expression levels of *avt* than subordinate males (Greenwood et al., 2008; Renn et al., 2008) (Fig. 3), collectively suggesting that AVT's influence is both social state-dependent and behavior-specific. Visual signals alone from a large dominant male are sufficient to fade body coloration in smaller dominant males for at least 7 days, but whole brain *avt* mRNA levels are only elevated for 3 days and there was no change in *avt* receptor levels (Chen and Fernald, 2011). These data suggest that visual stimuli alone are not enough to facilitate long-term AVT changes that are important for social state change. These manipulation and whole brain *avt* expression studies demonstrate a role for AVT signaling in regulating behavior and physiology associated with social position in *A. burtoni*, but because different AVT cell populations have different projection patterns and functions in most fishes (Greenwood et al., 2008; Larson et al., 2005; Saito et al., 2004), the mechanisms remain to be identified.

To better understand the role of AVT in regulating social status in *A. burtoni*, neuron population-specific investigations were performed. Dominant *A. burtoni* males had reduced *avt* expression in parvocellular, similar *avt* expression in magnocellular, and higher *avt* expression in gigantocellular POA regions compared to subordinate males, suggesting each AVT cell population influences the dominant phenotype differently (Greenwood et al., 2008) (Fig. 3). Across dominant and subordinate individuals, greater *avt* expression in parvocellular neurons was associated with fewer reproductive and aggressive behaviors, and more submissive fleeing, while more *avt* in gigantocellular neurons was associated with increased reproductive and aggressive behaviors (Greenwood et al., 2008). These data collectively suggested that parvocellular cells control subordinate behaviors, and gigantocellular cells play a role in promoting aggressive and courtship behaviors. More recently, this hypothesis was tested by comparing dual-labels of *avt* and *egr1*, an immediate early gene used as a neural activation marker, between dominant males engaged in fighting or courting. Fighting dominant males showed more activated magnocellular neurons than courting males but no differences in gigantocellular neurons (Loveland and Fernald, 2017). Therefore, the most current model suggests that parvocellular cells probably influence subordinate behavior in *A. burtoni*, and magnocellular cells, more-so than gigantocellular cells, are important for the control of agonistic behaviors.

Among other cichlid species and notably across vertebrates, AVT

neurons influence behavior and social state in a cell-population and species-specific manner. For example, while subordinate *C. dimerus* have larger parvocellular AVT neuron somata (Ramallo et al., 2012), subordinate *O. mossambicus* males have larger magnocellular and gigantocellular neurons compared to dominants (Almeida and Oliveira, 2015). In the monogamous convict cichlid *Amatitlania nigrofasciata*, general nonapeptide receptor antagonist given to males caused decreased affiliative behaviors towards potential mates (Oldfield and Hofmann, 2011), but AVT receptor antagonist increased affiliative courtship behaviors in male *A. burtoni* (Huffman et al., 2015). These differences among species suggest that the AVT system, while very conserved, differs in species with different reproductive strategies (e.g., monogamous vs polygamous vs cooperative breeding). Comparing the more closely related monogamous (*Herichthys cyanoguttatus)* and polygamous (*Herichthys minckleyi*) cichlids, there were no differences in telencephalic *avt,* telencephalic *v1a2 receptor*, or hypothalamic *avt* levels, but the polygamous, more territorial males had higher hypothalamic *v1a2* levels compared to monogamous males (Oldfield et al., 2013). This species difference suggests territorial defense behaviors are regulated by this *v1a2* receptor specifically. Overall, AVT is involved in control of behaviors and physiology associated with social state across cichlids, but species-specific patterns are common, suggesting different regulatory mechanisms associated with other variables like mating strategy.

Several studies also suggest the nonapeptide isotocin (IT) is important for male social hierarchies, but like AVT, there are often species-specific patterns. For example, *O. mossambicus* and *N. pulcher* show no differences in brain IT between dominant and subordinate males, suggesting IT does not directly affect social state in these species (Almeida et al., 2012; Reddon et al., 2015). In social cooperatively breeding *N. pulcher*, however, brain *it* mRNA levels are positively correlated with affiliative and submissive behaviors (O'Connor et al., 2016), but IT peptide levels in subordinates negatively correlate with general affiliation among conspecifics (Reddon et al., 2015), collectively suggesting that subordinates both express and turnover more IT than dominants. However, *N. pulcher* males injected with IT increase their aggression as rival male size increases, an effect opposing natural behavior (Reddon et al., 2012). This effect from IT is thought to be primarily linked to sensitized social signal processing that ultimately affects behavior rather than directly inducing aggression and is further supported by evidence implicating IT receptors for social habituation (Weitekamp et al., 2017c). When subordinate *N. pulcher* males are removed from their community for 4 h, injected with IT, and returned, they increase submissive behaviors, and are more likely to receive aggression and be evicted by the dominants (Hellmann et al., 2015). While subordinate behavior is often thought to assist the formation of social hierarchies by reducing the physical cost of conflict, these data suggest a more complex picture where IT-induced subordinate behavior can itself result in social conflict, but the reason for this effect is still unknown. Finally, comparisons between 8 closely related cichlids show that cooperative breeder species have fewer parvocellular IT cells (Reddon et al., 2017), a trend that contradicts other studies showing higher or no difference in whole brain *it* mRNA between social and non-social species (O'Connor et al., 2016; O'Connor et al., 2015), but could be explained by the hypothesis that social subordinates both produce and turnover more IT. In all, IT studies in cichlids suggest that IT is closely associated with social affiliation and subordinate behavior, illustrated by social species having more whole brain *it* (more IT synthesis), fewer parvocellular IT cells, and less whole brain IT peptide in subordinates (less IT storage and more IT turnover).

1.5.4. Somatostatin

Somatostatins are conserved across tetrapods (Liu et al., 2010), play important roles in regulating growth via inhibition of growth hormone secretion, and act as neuromodulators in the brain (Selmer et al., 2000). In cichlids, social status affects growth rate, which can influence social

rank (Heg et al., 2011; Hofmann et al., 1999; Hofmann and Fernald, 2000; Riebli et al., 2011). For example, *A. burtoni* males grow faster when either subordinate or socially ascending, and slower when dominant or socially descending (Hofmann et al., 1999). These growth changes were attributed to resource access and overall activity differences between social states, but subsequent studies in other cichlids show correlations between social state and growth that are independent of feeding and activity (Heg et al., 2011; Riebli et al., 2011). Because larger cichlids often assume dominance and are typically preferred by females (Kidd et al., 2013), these growth-related effects can impact social hierarchy dynamics. In *A. burtoni*, dominant males have larger somatostatin neuron somata in the hypothalamic preoptic area than subordinate and ascending males (Hofmann and Fernald, 2000) (Figs. 2,3). Because somatostatin inhibits growth, this supports previous evidence that dominant males grow more slowly (Hofmann et al., 1999). Intraperitoneal injections of somatostatin antagonist into dominant males also increases aggression (chases and border threats) in a dose-dependent fashion (Trainor and Hofmann, 2006), and somatostatin agonist reduces chasing behavior without affecting circulating T or 11-KT, collectively suggesting somatostatin has direct behavior-specific effects. In *A. burtoni*, therefore, POA somatostatin release may be inhibited in dominant males to promote aggression. Dominant *A. burtoni* also have increased expression of somatostatin pre-propeptide and somatostatin receptor 3 (*sstr3*) mRNA in the hypothalamus (Fig. 3), but no differences in the telencephalon (Trainor and Hofmann, 2007). However, *sstr2* levels in dominant males are negatively correlated with body size, demonstrating a role for *sstr2* in growth rate differences between social states, and that *sstr*s generally have receptor-specific effects on physiology. In conclusion, somatostatin plays direct and indirect roles in social hierarches by reducing aggression and negatively impacting growth rates in dominant males, representing a trade-off between growth and social rank.

1.6. Endocrine modulation of communication signaling, and sensory abilities used to acquire, assess, or maintain dominance

Acquiring and maintaining position in a dominance hierarchy requires that individuals constantly monitor their physical and social surroundings. Thus, incoming sensory information from conspecifics and the environment are crucial in societies with dominance hierarchies. For example, if a dominant cichlid is removed from a territory by predation, lower-ranking individuals must quickly detect and recognize this opportunity to rise in rank and gain territory ownership. It is also advantageous for lower-ranking individuals to monitor the dominance status of other group members to facilitate decisions on whether to engage in territorial disputes for access to limited resources like mates and shelters, or not to challenge others to prevent defeat or injury. Thus, many cichlids evolved the ability to predict their own position in the hierarchy, as well as the relative social rank of others, through observation and transitive inference (Desjardins et al., 2012; Grosenick et al., 2007). However, morphological structures used for signaling such as muscles, and sensory organs (e.g. eye, ear, nose) used for reception of communication signals can be dramatically influenced by an individual's internal state (Maruska and Butler, 2021a). This includes fluctuations in circulating hormone levels and changes in other modulatory substances or their receptors in the brain and peripheral sensory organs that can affect perception (Maruska and Butler, 2021b). One example of potential hormone modulation of signaling occurs in Mozambique tilapia (*O. mossambicus*) where males release pulses of urine to signal dominance status to both other males and females (Barata et al., 2008; Barata et al., 2007). Dominant males have larger more muscular bladders to store urine, and the potency of urine to stimulate the olfactory epithelium is positively correlated with male social status (Barata et al., 2007; Keller-Costa et al., 2012). While a direct causal link between bladder muscle hypertrophy and hormones is not known, hormones (e.g., sex-steroids, growth hormone) are well known for their

activational effects on muscles used for vocalizations and performance of visual displays across vertebrates (Brantley et al., 1993; Feng et al., 2010; Hall and Kelley, 2021; Smith et al., 2021). Thus, it is possible that higher circulating levels of androgens in dominant males contribute to their ability to signal dominance via urination.

In addition to chemosensory communication, there is evidence in cichlids that hormones regulate body coloration and pigmentation patterns that visually signal dominance and internal state. For example, dominant male *A. burtoni* are brightly colored (yellow or blue morphs) with a distinct black eye-bar associated with aggressive behaviors (Heiligenberg et al., 1972). Testosterone injections intensify head (e.g. black eye-bar) and body coloration and increase aggressive behaviors in male *A. burtoni* (Fernald, 1976) and AR knock-outs eliminate much of the bright male body colors (Alward et al., 2020), suggesting a link between endocrine signaling and dominance coloration. Male coloration is also an important visual signal used among neighboring territorial males because they differentially direct aggression towards neighbors based on their blue or yellow body color (Korzan and Fernald, 2007). In addition, injections of the pituitary hormone α-melanocyte-stimulating hormone (α-MSH) increase yellow body coloration by dispersal of xanthophore pigments in both color morphs but only increase aggression rates in blue males suggesting different regulation in each color morph (Dijkstra et al., 2017). Further, these pleiotropic effects on behavior and coloration indicate α-MSH may act centrally in the brain and peripherally in the skin. Because cichlids in general show diverse colorful body and fin patterns associated with social rank (e.g., subordinates typically lack bright coloration patterns) and they rely heavily on vision for social interactions, the role of hormones in regulating this dominance signal is likely very important for ultimately determining an individual's position in the hierarchy, their survival, and their reproductive success.

On the sensory reception side, examples come from *A. burtoni* where subordinate males may monitor the dominance status of other males in the population through chemosensory, visual, mechanosensory, and auditory signals (Butler and Maruska, 2015; Chen and Fernald, 2011; Maruska and Fernald, 2012; Maruska et al., 2012; Nikonov and Maruska, 2019). While there is little evidence to suggest that visual capabilities differ with male social status in this species (Butler and Maruska, 2021; Butler et al., 2019), the auditory and olfactory systems do differ between dominant and subordinate males at both peripheral and central levels (Maruska and Fernald, 2010b; Maruska et al., 2012; Nikonov et al., 2017; Nikonov and Maruska, 2019). For example, subordinate males have more sensitive hearing in the range of 600–800 Hz, which corresponds to the peak frequencies of courtship sounds produced by smaller males (Maruska et al., 2012). Because sound frequency is related to male body size, this acoustic information could allow low ranking males to monitor courtship activities to better choose males smaller than themselves to challenge for a territory. Levels of estrogen and glucocorticoid receptors in the saccule auditory endorgan are also greater in subordinate compared to dominant males, providing a possible hormone-mediated mechanism for this plasticity (Maruska and Fernald, 2010c).

Dominant males are also conspicuously colored and there is a trade-off between reproduction and vulnerability to predation associated with high rank, leading to differences in Mauthner neuron-mediated startle-escape behaviors in *A. burtoni* (e.g. higher responsiveness in dominants) (Neumeister et al., 2010). The Mauthner neurons (or M-cells) receive inputs from multiple sensory systems (auditory, lateral line, visual), and serotonin acting at the M-cells via the 5-HT receptor subtype 2 modulates this startle responsiveness related to social status (Whitaker et al., 2011). Specifically, both startle-escape behavior and M-cell physiology are modulated by 5-HT, leading to status-specific differences related to survival and reproductive success.

Chemosensory communication is important for both intra- and inter-sexual communication in cichlids, and the olfactory system also varies with male social status in *A. burtoni*, which may be used to maintain dominance and may be modulated by hormones (Field and Maruska, 2017; Field et al., 2018; Maruska and Fernald, 2010b, 2012; Nikonov et al., 2017; Nikonov and Maruska, 2019). For example, olfactory-sensitive neurons in the forebrain (Vv, ventral nucleus of the ventral telencephalon) of subordinate males are more responsive to male-released compounds compared to dominants, suggesting they may monitor the relative rank of other males in the population (Nikonov and Maruska, 2019). This would allow them to better choose which lower-ranking individuals to challenge for a territory, thereby reducing chances of physical injury and a fall in social rank. In contrast, neurons in the forebrain of dominant males are more sensitive to female-released odorants, which helps them determine female ovulation status to improve reproductive fitness while they hold a territory (Nikonov and Maruska, 2019). While a direct link to hormones mediating these olfactory differences is lacking, the levels of sex-steroid receptors in the olfactory bulbs and in this same forebrain olfactory region do differ between dominant and subordinate *A. burtoni* males, suggesting different steroid sensitivity (Maruska and Fernald, 2010b; Maruska et al., 2013b). Recordings of local field potentials (LFPs) in this Vv forebrain region also demonstrate greater synaptic inputs in dominant males suggesting status-dependent differences linking olfactory and other neural inputs to goal-directed behaviors (Nikonov and Maruska, 2019). Collectively, this may provide a flexible mechanism for switching the neural circuitry to improve detection of specific olfactory signals important for their current position in the hierarchy while also allowing rapid transitions between social ranks. This type of endocrine-mediated sensory plasticity revealed in auditory and olfactory systems of *A. burtoni* may be more widespread across cichlid species than currently realized and adds another layer of complexity to understanding how dominance hierarchies are established and maintained within a population.

Living in large social groups with frequent dynamic interactions among individuals also often favors evolution of enhanced cognitive abilities. Several studies in different cichlid species document remarkable cognitive capabilities that could facilitate establishment and maintenance of dominance hierarchies (Kohda et al., 2015; Stanbrook et al., 2020; Wallace and Hofmann, 2021). For example, the rock-dwelling Tanganyikan cichlid *Julidochromis transcriptus* can discriminate between familiar and unfamiliar conspecifics using facial patterns alone (Hotta et al., 2017), Nile Tilapia exhibit inhibitory control (a measure of cognitive flexibility) (Brandao et al., 2019), and transitive reasoning is used in several species to infer social rank and contest ability of other individuals within the hierarchy (Grosenick et al., 2007; Hotta et al., 2015). How these cognitive tasks are performed and potentially regulated by endocrine and neuroendocrine factors, however, remains relatively unexplored in cichlids.

2. Female social hierarchies

Compared to the extensive work on hormones and male cichlid social hierarchies, relatively little is known about endocrine regulation in female hierarchies. In *A. burtoni* the natural female hierarchy remains undefined. However, females housed without males for several weeks will form a clear social hierarchy that mimics the male social ranks (Renn et al., 2012). Dominant females will adopt dominant male-typical coloration patterns (eyebar), aggressive/territorial behaviors (chases, lateral displays, border threats, digging), reproductive courtship behaviors towards other females, and hormone changes (increased circulating testosterone and estradiol) that are not seen in subordinate females (Renn et al., 2012). Unlike the males though, dominant females do not suppress the gonadal physiology of the subordinate females, who still develop mature ova and can spawn. Interestingly, the dominant status of females typically lasted about the length of 1 reproductive cycle and was often lost after spawning, suggesting a link between the reproductive cycle and female social state/behavior. More studies with *A. burtoni* females support a reproductive link to social state because gravid, reproductively ready females with high circulating progesterone

are more aggressive (O'Connell et al., 2013a) and direct most aggression towards brooders (Field and Maruska, 2017). Similarly, reproductively ready *C. dimerus* females show the highest aggression of all reproductive states and have the highest levels of circulating testosterone, 11-KT, and estradiol (Tubert et al., 2012). Further, winners of social challenges who likely benefit from increased aggression also have increased estradiol (Scaia et al., 2018). Lastly, female *N. pulcher*, who have defined social hierarchies, behave like dominant males and have similarly high levels of testosterone and AVT compared to subordinate males (Aubin-Horth et al., 2007). In cichlids, this pattern of "masculinized" hormonal profiles in females approaching reproductive readiness seems conserved, but the structure of female social hierarchies and direct effects of these hormonal changes on the social ranks are unknown. Future work on the control of female social dynamics across cichlids is important to expand our understanding of how the endocrine system might play simultaneous roles in regulating the female reproductive cycle, behavior, and social rank to impact success and diversity.

3. Conclusions and future directions

In this review we summarized many aspects of endocrine and neuroendocrine systems that are associated with dominant and subordinate social positions within male cichlid dominance hierarchies. While our current knowledge on this subject is dominated by studies in only a few representative cichlid species, particularly *A. burtoni*, the widespread existence of social hierarchies among cichlids in general makes them excellent systems for future investigations. In *A. burtoni*, and likely other species, the decision to rise or fall in relative social rank is dictated by behavioral interactions with conspecifics (including observations of interactions among others to assess their relative rank) in the population, sensory inputs via multiple channels, and internal physiological state. Signaling molecules in the brain such as GnRH1, nonapeptides, 5-HT, CRH, somatostatin, steroids, and many others may all play a complex role in facilitating a male's transition towards adopting the behaviors, coloration, and reproductive physiology needed to support their new role in the hierarchy. The plasticity of these endocrine and neuroendocrine processes is remarkable, occurs at multiple levels of biological organization, and is evident in both the brain and peripheral organs. This highlights the importance moving forward of studying dominance hierarchies from a more organismal point of view and making collaborative efforts to synthesize previous results with new studies within a particular species. Further, periodic reviews such as this that consolidate what is known about dominance hierarchies in cichlids are valuable to identify which future directions might provide the most transformative advancements in our understanding of the links between endocrine systems and social rank.

Many avenues for future research exist in cichlids to further our understanding of how dominance hierarchies might be regulated and maintained by endocrine and neuroendocrine systems. An expanded comparative approach in cichlids that includes more species with different hierarchy structures (e.g., male only, female only, mixed sexes) is important to resolve some of the conflicting results related to hormones and social rank. Comparative phylogenetic methods typically use information on the historical relationships among lineages to test evolutionary hypotheses. For example, field-collected males and females of four closely related Ectodini cichlid species representing two independent evolutionary transitions from polygyny to monogamy, used a comparative neural transcriptomic approach to test the hypothesis that these independent transitions recruited similar gene sets (Renn et al., 2018). Further, a meta-analysis using datasets of high-throughput expression profiling on social dominance in fishes across social contexts, sex, and species revealed associations between neural gene expression profiles and social dominance (Renn et al., 2016). As more large datasets on hormone and neuroendocrine profiles (at genomic, transcriptomic, and proteomic levels) become available in cichlids with diverse social hierarchies, these types of comparisons should reveal

regulators that are species-specific as well as those that are common to dominant and subordinate social ranks among different cichlid species, or across vertebrates more generally. Comparative results, however, are further complicated by differences in mating strategies and parental care among cichlid species that also must be disentangled moving forward. Nevertheless, the importance of endocrine system traits to the evolution of social hierarchies would be a rewarding area of future research in cichlids because of their diversity.

Differences in experimental designs must also be carefully considered when making broad generalizations about the role of hormones in dominance hierarchies, including definitions of dominance; for example, is dominance strictly defined by an individual's behavior/interactions with other group members, or by certain non-behavioral phenotypic characteristics like coloration, or both, and how do winner-loser effects and prior experience contribute to these definitions? Clearly defining the criteria for dominance related to endocrine measures should be a priority in all published studies to facilitate comparisons. In group-living cichlids where dominance hierarchies develop, it seems prudent to define dominance based on agonistic behavioral interactions resulting in a dominant winner and subordinate loser, as historically proposed, especially since most physiological and morphological phenotypic traits arise from the outcome of these interactions rather than cause them. This definition would then focus future work on understanding the *timing* of phenotypic changes associated with endocrine and neuroendocrine systems following the winner-loser outcome. Studies using social network analyses to examine community structure will also contribute valuable information towards understanding hormonal impacts on all individuals within a community rather than only the most dominant and most subordinate.

Much of the existing research has also treated each hormonal (or neuroendocrine) system in isolation, but we know many of these systems interact at multiple levels. Thus, more integrative studies that measure multiple physiological variables in the same individuals are needed to provide insights on the complexities of endocrine regulation of dominance. Towards this goal, many -omics approaches (e.g., genomics, transcriptomics, proteomics, metabolomics) will be valuable for better understanding the integration and interconnectedness of different endocrine systems and how they contribute to social rank. Further, the role of epigenetics, microRNA regulation, and other regulatory mechanisms in establishing, maintaining, or transitioning individuals' social positions are not well understood. Because the expression of behaviors necessary for maintaining a social position is ultimately controlled by the brain, future work should also focus on identifying the specific neural circuits involved in integrating sensory inputs, decisions, central regulation of physiological changes that alter HPG and HPI axes, and behavioral outputs. As mentioned above, cognitive ability is important in dominance hierarchy formation and future work studying the neuromolecular, endocrine, and neuroendocrine mechanisms of cognition would be valuable.

While much of the information summarized in this review provides data on different physiological measures associated with a particular social status like dominant or subordinate, what remains unclear in most cases are the mechanistic details. For example, if dominant males typically have higher circulating sex-steroid levels and greater HPG axis activity, what sensory and neural mechanisms lead to this and what role do they play in allowing that individual to acquire or hold his position in the dominance hierarchy? For many of the abovementioned future directions, developing technologies such as CRISPR/Cas9 gene editing, functional genomics, in vivo microscopy, optogenetics, chemogenetics, artificial intelligence, pharmacological manipulations, and others promise to provide more direct functional information on how signaling molecules in the brain and other tissues contribute to dominance phenotypes and behaviors. Moving forward, cichlids will provide many insights on the interactions between hormones and dominance hierarchies that can be used as comparative tools to better understand the selective pressures leading to the evolution of these complex social

societies across vertebrates.

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