

Evolution of stress responses refine mechanisms of social rank

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ABSTRACT

Social rank functions to facilitate coping responses to socially stressful situations and conditions. The evolution of social status appears to be inseparably connected to the evolution of stress. Stress, aggression, reward, and decision-making neurocircuitries overlap and interact to produce status-linked relationships, which are common among both male and female populations. Behavioral consequences stemming from social status and rank relationships are molded by aggressive interactions, which are inherently stressful. It seems likely that the balance of regulatory elements in pro- and anti-stress neurocircuitries results in rapid but brief stress responses that are advantageous to social dominance. These systems further produce, in coordination with reward and aggression circuitries, rapid adaptive responding during opportunities that arise to acquire food, mates, perch sites, territorial space, shelter and other resources. Rapid acquisition of resources and aggressive postures produces dominant individuals, who temporarily have distinct fitness advantages. For these reasons also, change in social status can occur rapidly. Social subordination results in slower and more chronic neural and endocrine reactions, a suite of unique defensive behaviors, and an increased propensity for anxious and depressive behavior and affect. These two behavioral phenotypes are but distinct ends of a spectrum, however, they may give us insights into the troubling mechanisms underlying the myriad of stress-related disorders to which they appear to be evolutionarily linked.

1. Function of social rank

On the high plains of Africa, where human primates are thought to have evolved (Wynn, 2004), current non-human primate residents, such as the olive baboon, live in complex and dynamic social constructs with status and stress relationships tightly interwoven (Sapolsky, 1982, 1987, 1991). Within the social hierarchy, dominant males accrue copulatory, aggressive, and food competition successes, along with unique gestural interactions. While these status parameters are highly intercorrelated, they do not correlate with aggressiveness or frequency of fighting. In fact, social dominance is also not correlated with the sex steroid testosterone (T), but is revealed by the timing and rate of change in both T and the adrenocortical stress steroid cortisol. Although plasma cortisol concentrations in dominant males are typically low, they rise rapidly and to a greater extent in response to stress, as do T levels (Sapolsky, 1982, 1983, 1988). Subordinate status results in chronically elevated plasma cortisol, with reduced testicular function and reproductive success (Sapolsky, 1985, 1988, 1989, 1990). However, during periods of

social instability, adrenocortical function is modified differentially depending on the upward or downward trajectory of status (Sapolsky, 1992). Thus, social status is only temporarily stable, and its dynamic projection depends on stress-related changes in hormones and neurotransmitters (Fig. 1) (Blanchard et al., 1995; Monder et al., 1994; Sapolsky, 1992; Summers et al., 2005a, 2005b, 2005c).

While this example from a near relative sets the stage for understanding the neurobiological mechanisms that regulate social status, the evolutionary arc for the development of the suite of adaptive behaviors that result in dominant and subordinate relationships is very wide. That is, social rank relationships are widespread among animal groups, such that hierarchies or dominant-subordinate relationships are found among invertebrates like crayfish (Huber et al., 2001) and lobster (Karavanich and Atema, 1998), and in vertebrate classes from fish to birds, rodents, elephants, and primates, including humans (Christian, 1968; DiBattista et al., 2005; Dinzberg et al., 1992; Ejike and Schreck, 1980; Greenberg et al., 1984a; Hofmann et al., 1999; Korzan and Summers, 2007; Lorenzi et al., 2009; Maruska et al., 2012, 2019; McIntyre and Chew, 1983;

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Morgan et al., 2000; Nevison et al., 1996; Santamaria-Garcia et al., 2015; Semsar et al., 2001; Winberg et al., 1991, 1997; Wittmyer et al., 2008). In some species, the communal confrontations necessary to generate rank relationships produce enough emotional activation through social stress to realize cardiac health-related responses (Klemfuss et al., 1998; Sgoifo et al., 1999). Thus, the functional benefits and disadvantages of rank discrimination include such diverse aspects of fitness as daily rhythms of heart rate, body temperature, and activity, as well as reproductive success, stress responsiveness, and depression (Blanchard et al., 1995; Meerlo et al., 1999; Sapolsky, 1982; Sloman et al., 2002).

Additionally, social rank relationships are not restricted by sex. Female sex rank relationships are found in numerous species, including hyenas (Lewin et al., 2014), African elephants (Freeman et al., 2010), rock hyrax (Koren et al., 2006), Bighorn Sheep (Festabianchet, 1991), reindeer (Holand et al., 2004), pigs (Hjarvard et al., 2009), rats (Militzer and Reinhard, 1983), and many types of primates (Foerster et al., 2011; Johnson et al., 2014; Kromrey et al., 2014; Lu and Borries, 2004; Renevey et al., 2013) like baboons (Mueller, 2005), chimpanzees (Riedel et al., 2020), and Rhesus macaques (Nevison et al., 1996; Zehr et al., 2005). Among mammals, some species, including elephants, hyenas, some lion prides, European bison, and bonobos have been suggested to be matriarchal, with females holding higher status and hierarchical positions. Numerous non-mammalian species also exhibit female social status hierarchies or dominant-subordinate relationships, including Jungle Fowl (Chappell et al., 1999), black-capped chickadees (Ramsay and Ratcliffe, 2003), the green anole lizard *Anolis carolinensis* (Andrews and Summers, 1996), and the bluehead wrasse (Price et al., 2018). In a reptilian example, females of the lizard *A. carolinensis* compete for access to males (Andrews and Summers, 1996). Paired females exhibit aggressive social behavior (assertion, challenge, displacement, attacks, and bites) which contributes to the development of dominant-subordinate relationships. Dominant females respond to courtship significantly more often than subordinate females, indicating receptivity. In cichlid fish, gravid females have increased sensitivity to dominant male courtship coloration (Butler et al., 2019). Dominant,

typically larger, females also maintain ovarian cycling and growth (Summers et al., 1995), which is inhibited in smaller, subordinate females by the stress hormone adrenocorticotrophic hormone (ACTH) and subsequent corticosterone secretions (Summers, 1995). However, dominant status, rather than reproductive activity, appears to be regulated by heightened limbic serotonergic and dopaminergic activity in females (Summers et al., 1997) and males (Summers and Greenberg, 1995). Thus also, are stress responsiveness and resiliency, as well as reproductive success or failure, associated with social status in females and in males (Price et al., 2018; Sapolsky, 1982; Summers, 1995).

Status or rank functions as a social mechanism to coordinate behavioral output of populations when the acquisition of resources requires competition and/or evasion of predators, and is therefore stressful (Blanchard et al., 1995, 2001b; Blanchard and Blanchard, 1989b; Monder et al., 1994; Summers and Winberg, 2006; Tamashiro et al., 2005). Establishing the roles of stress neurocircuitries and molecular mechanisms associated with the establishment of social rank relationships has been facilitated by innovations of novel conceptual models, such as the Visible Burrow System, Social Defeat, Conditioned Defeat, or Stress Alternatives Model (Blanchard et al., 2013; Huhman et al., 2003; Krishnan et al., 2007; Pearson et al., 2017; Potegal et al., 1993; Robertson et al., 2015; Yaeger et al., 2020). Thus, we suggest that inter-individual rank relationships are formed and shaped by environmental and socially stressful conditions, and mediated by the neurocircuitries (Fig. 1) that regulate stress and aggressive responsiveness (Summers and Winberg, 2006). For these reasons also, change in social status can occur very rapidly (Burmeister et al., 2005).

1.1. Social relationships are stressful

Although social relationships are stressful, in the classic Selye eustress/distress sense (Selye, 1984, 1985), rank relationships are stressful by the nature of status interactions (Sapolsky, 1982, 1987, 1992). It is important to begin with the idea that in populations, there are individual differences in neuroendocrine stress responsiveness (Meaney et al., 1993; Wood et al., 2010). These differences are also seen

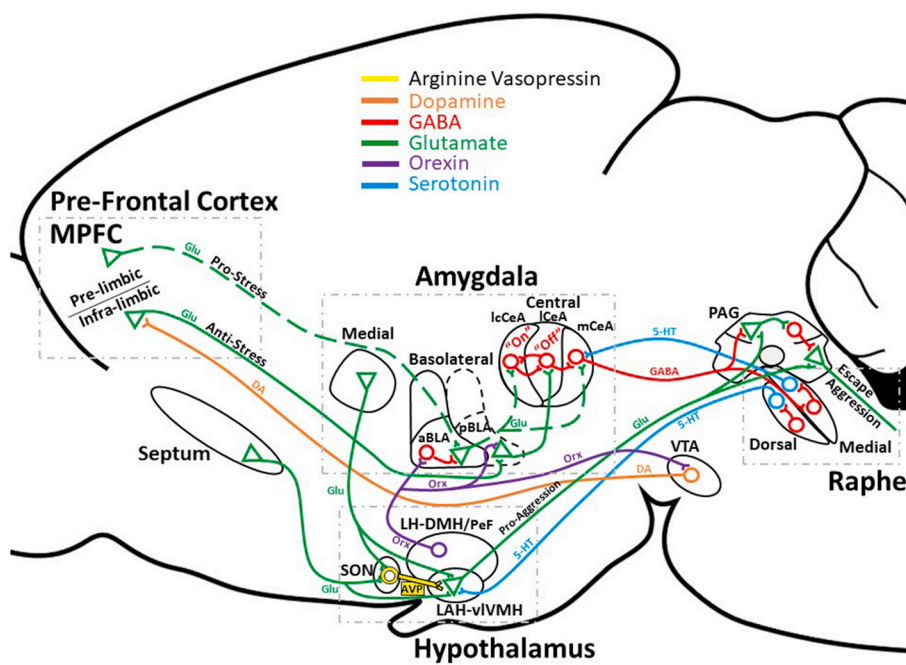


Fig. 1. The interactive nature of stress, aggression, reward, and decision-making neurocircuitries are depicted as they exist in the mouse brain. Linear stress circuitry includes mPFC-BLA-CeA-dPAG-vPAG, but also includes branching connections from LH/VMH-PeF, plus (not shown) to hippocampus, VTA, and nucleus accumbens (NAc). Linear aggression circuitry includes MeA & Septum-LAH/viVMH-dPAG and vPAG, but also includes AVP branches from SON, and others from mPFC and hippocampus (not shown). Ascending circuitry for decision-making includes BLA-mPFC (reciprocal neurons to stress neurons depicted), as well as branches to other cortical regions and hippocampus (not shown). Ascending Reward circuitry includes VTA-NAc (not shown) & mPFC (orange). Legend: Arginine Vasopressin (AVP) in yellow, Dopamine (DA) in orange, γ -Aminobutyric acid (GABA) in red, Glutamate (Glu) in dashed green (pro-stress) and light green (anti-stress), orexin (Orx) in purple, and serotonin (5-HT) in blue. Anatomical regions: aBLA = anterior basolateral amygdala, lCCEA = laterocapsular central amygdala, lCEA = lateral central amygdala, LH/DMH-PeF = orexinergic lateral hypothalamus/dorsomedial hypothalamus – perifornical Area, mCeA = medial central amygdala, mPFC = medial Prefrontal Cortex, PAG = periaqueductal gray, pBLA = posterior basolateral amygdala, SON = supraoptic nucleus, VTA = ventral tegmental area. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

between sexes (Bangasser and Valentino, 2012; Bangasser, 2013; Grafe et al., 2019; Valentino et al., 2012; Weintraub et al., 2010), and are influenced by individual stress histories (Vining et al., 2007). There are several additional reasons that social rank relationships may be traumatic and differentially stressful, but the primary reason is that these relationships determine the level of access to resources for each individual of a population (Blanchard et al., 1995). Those resources, such as food, water, shelter, perching/displaying/basking sites, and mates, determine not only fitness, but existence (Blanchard and Blanchard, 1989b, 1990). As such, these interactions create distress. Additionally, the social interactions that determine rank relationships are unpredictable in timing, content, and intensity (Summers et al., 2005a). While, the unpredictability of rank-determining social interactions is different for dominant as compared to more subordinate individuals, they are stressful, nonetheless, for all individuals, regardless of rank (Øverli et al., 1999; Sapolsky, 1982; Summers et al., 2003). This suggests that for social species, at least, there is no aspect of life which does not involve some element of stress. Thus, the impact of stress neurocircuitries on neural functions which regulate those specific aspects of life is significant. That is, social rank and the stress it generates, become critical elements in the life history and survival of these species, regulated by the balance of pro-stress and anti-stress components of the essential neurocircuitries (Fig. 1) (Yaeger et al., 2020).

The stress neurocircuitry involved in social status relationships involves three systems (Fig. 1). The first begins with reciprocal connections between basolateral amygdala (BLA) and prefrontal cortex (PFC). These areas contain both pro-stress, and anti-stress regions that can be identified by the stress-associated genetic markers *Ppp1r1b* (DARPP32) and *Rspo2* (R-Spondin 2) in BLA (Kim et al., 2016), and *Drd1* (D₁ receptor) in PFC (Hare et al., 2019). The BLA, which is necessary for learning related to fearful and aversive events (Orsini and Maren, 2012), is divided into anterior (aBLA expressing *Rspo2*) and posterior (pBLA expressing *Ppp1r1b*) regions; with the anterior region promoting stress responses (pro-stress), and the posterior region limiting stress (anti-stress) (Kim et al., 2016). Both anterior and posterior BLA include excitatory (glutamatergic, Glu) circuits in which the BLA receives input from limbic and cortical structures, and also projects to the principal output of the amygdala, (medial portion of the Central Amygdala; mCeA), which produces learning and expression of pro-stress responses, especially to hypothalamus and the periaqueductal gray (PAG) (Bhatnagar et al., 2004). Inputs to the aBLA and pBLA from the PFC, come from functionally distinct sources. Pro-stress input from prelimbic PFC (PrL) projects to the pro-stress *Rspo2* expressing neurons in the aBLA (Kim et al., 2016). The infralimbic (IL) portion of the mPFC projects anti-stress signaling, from dopamine receptor *Drd1* expressing neurons (Hare et al., 2019), which impinge on *Ppp1r1b* expressing neurons in the pBLA (Kim et al., 2016). This anti-stress system is promoted by second main system, dopamine (DA) activity from reward circuits that include the VTA projecting to the nucleus accumbens (NAc), but also to PFC, hippocampus, and other limbic regions (Hare et al., 2019; Lozano-Montes et al., 2019; Tovote et al., 2015). In the third system, reciprocal innervation from aBLA and pBLA designated neurons projects to specific neurons in the hippocampus (Li et al., 2018; Pi et al., 2020; Yang et al., 2016), and its alternative connections to the PFC (Eichenbaum, 2017; Goldman-Rakic et al., 1984). Together, the systems reveal a pan-limbic relationship to environmental and social stress regulation (Blanchard et al., 2001a; Yang and Wang, 2017). To us it seems unlikely that any element of these three systems ever acts independently of the others. Thus, social stress regulation is manifest through a balance of pro- and anti-stress systems, as well as interwoven decision-making circuitry (Fig. 1) that results in meaningful and adaptive behavioral responses (Gonzalez-Martinez et al., 2017; Smith et al., 2014; Yaeger et al., 2020; Yang et al., 2016).

The stressful effects of the establishment of social rank relationships have been demonstrated in experiments from the previously mentioned models to significantly influence, or be influenced by a large number of

different, but related (through neurocircuitry; Fig. 1), transmitters, neuromodulators, neurotrophins, and other factors (Table 1).

Though most of these relationships have been determined in laboratory settings, similar monoaminergic activity changes have also been demonstrated in response to social rank establishment stress in lizards in the wild (Matter et al., 1998).

1.1.1. Aggression is stressful

Of course, one of the main reasons that social interactions are stressful, is that a common element in those exchanges, especially rank-related activity, is aggression. Aggression is inherently stressful, and dangerous. Studies in all types of species demonstrate that aggressive interaction promotes stress responses from neuroendocrine systems (Blanchard et al., 1995; Lucas et al., 2004; Monder et al., 1994; Øverli et al., 2004b; Smith et al., 2016; Summers, 2001, 2002; Summers et al., 2005b, 2005c; Summers and Winberg, 2006). Importantly, the activity of those neural and endocrine responses also modifies social aggression (Backström et al., 2011a; Blanchard et al., 2005; Carpenter et al., 2009; Farrokhi et al., 2004; Griebel et al., 1995; Lepage et al., 2005; Øverli et al., 2002a, 2002b; Schjolden et al., 2009; Wall et al., 2004a; Winberg et al., 2001). While the transmitter systems and brain regions active during social interaction/rank development stress are recapitulated in any listing related to aggression, since these two behavioral elements are typically coincidental, there are studies that examine stress responsiveness specifically during aggression. Those studies sometimes address neurotransmitter changes before the agonistic encounter (in pre-determined behavioral phenotypes), and then compare them with measurements taken during aggression (Summers et al., 2005b). There are studies that parse out temporal changes in hormone and transmitter activity, including the intervals immediately after the aggression begins (Øverli et al., 1999, 2004a; Schuurman, 1980; Summers, 2001, 2002; Summers et al., 2003, 2005c). Numerous studies examine the effects of targeted drugs, and sometimes their effects in specific brain regions, to determine the neural effects on aggression itself (Backström and Winberg, 2009; Backström et al., 2011a; Blanchard et al., 1987a, 1987b; Carpenter et al., 2009; Carrillo et al., 2011; Cooper et al., 2009; de Almeida et al., 2008; de Boer and Koolhaas, 2005; Delville et al., 1996a, 1996b; Dodman et al., 1996; Ferris and Potegal, 1988; Ferris et al., 1992; Ferris, 1996; Fish et al., 2008; Grimes and Melloni, 2005; Grimes et al., 2006; Harmon et al., 2002; Harrison et al., 2000a, 2000b; Jasnaw et al., 2002; Larson and Summers, 2001; Lee et al., 2021; Lepage et al., 2005; Melloni and Ricci, 2010; Miczek et al., 1993, 1995, 1998; Morrison et al., 2015, 2020; Øverli et al., 2002a, 2002b; Ricci et al., 2004, 2005, 2007; Schjolden et al., 2009; Schwartz et al., 2009; Schwartz and Melloni, 2010a, 2010b; Summers and Winberg, 2006; Veiga et al., 2007; Winberg et al., 2001). There are also a few studies in which neural and endocrine measurements are taken in the wild (Sapolsky, 1982, 1983, 1985, 1989, 1992) as well as during aggression (Matter et al., 1998). There have also been studies on aggression in captured feral rodents (Benus et al., 1991; de Boer et al., 2003; Everts et al., 1997; Sgoifo et al., 1996). The results of these studies suggest that both aggression (see section 2.3.) and stress neurocircuitries (Fig. 1) are activated during aggressive bouts.

1.1.2. Definition of dominance

Social dominance is a temporary state of the highest rank, which is not genetically defined, but arises from advantages accrued through genetic and epigenetic adaptations, physiology, developmental maturation and timing, metabolic resources and reserves, temporary or long-term environmental conditions, social dynamics, and circumstance (Ricci et al., 2013). Social dominance is the key in social rank relationships, although it may be a minority position in larger social hierarchies.

1.1.3. Relationship between dominance and rank

Since rank relationships are temporary and fluid, the social

Table 1
Neurochemicals acting in brain regions to influence social rank relationships.

Neuroactive Element	Brain Area Influenced by Neuroactive Element to influence Social Rank	References
AVP	Amygdala (Medial) Hippocampus (CA2) Hypothalamus (PVN, POA)	(Albeck et al., 1997; Backström and Winberg, 2009; Backström et al., 2011b; Caldwell et al., 2017; De Goeij et al., 1992; Dewan et al., 2011; Dewan and Tricas, 2011; Erhardt et al., 2009; Gesto et al., 2014; Huang et al., 2020; Larson et al., 2006; Ross et al., 2019; Shalev et al., 2011)
BDNF	Amygdala (Basal Lateral, Central, Medial) Hippocampus Mesolimbic DA pathway (Nucleus Accumbens, VTA) Prefrontal Cortex	(Berton et al., 2006; Fanous et al., 2011; Jiang et al., 2014; Mallei et al., 2019; Moravcova et al., 2020; Nasrallah et al., 2019; Nikulina et al., 2012; Nowacka et al., 2014; Razzoli et al., 2011; Smith et al., 2014; Taylor et al., 2011)
Cannabinoids	Hippocampus	(Robertson et al., 2017)
CRF	Amygdala (Medial, Central) Hypothalamus (VMN, POA, PVN) Raphé (Dorsal Nucleus)	(Backström et al., 2011a; Backström et al., 2011b; Backström and Winberg, 2013; Carpenter et al., 2009; Doyon et al., 2003; Elliott et al., 2010; Fekete et al., 2009; Hostetler and Ryabinin, 2013; Keeney et al., 2006; Lukkes et al., 2009; Moltesen et al., 2016; Ruis et al., 1999; Wood et al., 2010; Wood et al., 2013)
DA	Amygdala (Lateral, Medial) Hypothalamus Locus Ceruleus Mesolimbic DA pathway (Nucleus Accumbens, Dorsal Striatum, VTA) Prefrontal Cortex (Medial) Raphé Septum Caudate Putamen Substantia Nigra	(Berton et al., 2006; Korzan and Summers, 2007; Lucas et al., 2004; Nocjar et al., 2012; Shimamoto et al., 2011; Tidey and Miczek, 1996; Watt et al., 2007; Winberg and Nilsson, 1992)
ΔFosB	Hippocampus (Ventral) Mesolimbic DA pathway (Nucleus Accumbens) Prefrontal Cortex	(Eagle et al., 2020; Mul et al., 2018; Wang et al., 2013)
Epinephrine	Hippocampus Mesolimbic DA pathway (VTA)	(Ling et al., 2010)
GABA	Amygdala (Basal Lateral, Central [Medial, Lateral], Medial) Hippocampus Hypothalamus Mesolimbic DA pathway Bed Nucleus of the Stria Terminalis Prefrontal Cortex (Medial)	(Tsukahara et al., 2019; Xu et al., 2020; Yaeger et al., 2020)
Glutamate	Hippocampus (CA3, Ventral) Prefrontal Cortex (Medial)	(Eagle et al., 2020; Krugers et al., 1993; Park et al., 2018)
Neuropeptide S	Amygdala (Basal Lateral, Central) Hypothalamus	(Kumsta et al., 2013; Smith et al., 2014; Zoicas et al., 2016)
Neuropeptide Y	Amygdala (Basal Lateral) Hypothalamus (POA) Striatum (Dorsal) Caudate Putamen	(Doyon et al., 2003; Panksepp et al., 2007; Sajdyk et al., 2008)
NE	Hippocampus Hypothalamus Locus Ceruleus	(Anisman and Sklar, 1981; Bingham et al., 2011; Chajale et al., 2013; Matter et al., 1998; Watt et al., 2004)
Orexin/ Hypocretin		(Eacret et al., 2019; Nocjar et al., 2012; Staton et al., 2018;

Table 1 (continued)

Neuroactive Element	Brain Area Influenced by Neuroactive Element to influence Social Rank	References
Serotonin	Amygdala (Basal Lateral) Hippocampus	Summers et al., 2020; Yaeger et al., 2020)
	Hypothalamus (Lateral) Amygdala (Medial) Hippocampus (CA1, CA3, CA4, Dentate Gyrus) Hypothalamus Mesolimbic DA pathway (Nucleus Accumbens, VTA) Locus Ceruleus Raphé (Dorsal, Interfascicular, Median) Striatum	(Backström and Winberg, 2017; Chung et al., 1999; Cubitt et al., 2008; Ferris, 1996; Korte et al., 1990; Korzan and Summers, 2004; Larson and Summers, 2001; Lepage et al., 2005; Matter et al., 1998; McEwen, 2000; McKittrick et al., 1995; McKittrick et al., 2000; Moltesen et al., 2016; Summers and Greenberg, 1995; Summers, 2001; Summers et al., 2004; Winberg et al., 1991; Winberg et al., 1992; Winberg et al., 1993; Winberg and Nilsson, 1993; Winberg et al., 1997; Winberg and Lepage, 1998; Zou et al., 2020)

relationships and impact on stress responsiveness are somewhat dependent on the number of individuals vying for rank superiority. While most investigations into social rank in the laboratory are carried out by employing aggressive dyads, most socially competitive relationships in natural settings are more variable. What that means in terms of social stress experienced by the individuals competing is important, because, in the dyad, it is an all-or-nothing competition, and the distinctions between dominant and subordinate individuals in stress hormone and neurotransmitter concentrations are maximized, as are the patterns of their release (Summers et al., 1998, 2003, 2005b, 2005c; Summers, 2001). What is more, even among aggressive pairs, the consequences of social aggression are unpredictable and uncontrollable (Summers et al., 2005a), making this type of stressor particularly intense (Anisman and Sklar, 1981; Baratta et al., 2007; Jones and Fernyhough, 2007; Koolhaas et al., 1997a; Rozeske et al., 2011). Additional competitors and complex environmental conditions, can provide some forms of buffer for the uncontrollable and/or social stress involved (Amat et al., 2006; Christianson et al., 2009, 2011; Greenwood et al., 2005; Kiyokawa et al., 2007). For example, social play is sufficient to attenuate the effects of social stress (Burlinson et al., 2016). Exercise (such as wheel running) and environmental enrichment also mitigate the effects of social defeat (Greenwood et al., 2005). One of those mitigating circumstances is the existence of territories, and the dynamics of territoriality.

1.1.4. The role of territoriality in social rank

There is nothing *per se* about social rank relationships that requires that spatial relationships for individuals or groups would also be modified, however, the price of defending resources becomes ever more costly as the range over which they must be defended grows. Thus, territoriality becomes an evolutionarily adaptive strategy, such that dominance over a territorial space reduces the cost of resource defense by decreasing interactions with conspecifics. Territorial behavior is linked to stress neurocircuitry and signaling, by which responsiveness to intrusion may be regulated (Fokidis and Deviche, 2012).

1.2. Stress coping strategies for social status

For all social animals, the benefits of close proximity of conspecifics is tempered by the management of agonistic socially induced stress, especially for lower status individuals. For this, species evolve stress coping strategies (Koolhaas et al., 1999, 2007, 2011; Øverli et al., 2007).

Individual adaptive capacity and vulnerability to stress-related social conflict and disease (Koolhaas et al., 1999) has tremendous importance for understanding dominant-subordinate relationships, as both produce specific and similar behavioral phenotypes (Korzan and Summers, 2007; Øverli et al., 2007). Wild or feral populations contain individuals exhibiting proactive or reactive coping styles, playing important roles in species population ecology (Koolhaas et al., 1999), and conferring differential fitness consequences under divergent environmental conditions (Coppens et al., 2010). Divergent behavioral flexibility between phenotypes mediated by circuitry involving dopaminergic and serotonergic input to PFC (Coppens et al., 2010) is likely informed by the balance in pro- and anti-stress, motivational, and decision-making circuits (Yaeger et al., 2020). This relatively ubiquitous circuitry is capable of producing a wide variety of behavioral outcomes across a diverse array of species. One example of a common passive strategy is to change appearance, essentially allowing them to hide. For example, in the African cichlid fish *Astatotilapia burtoni*, non-territorial males have a specific mechanism (Francis et al., 1993) to decrease aggressive behavior directed toward them; first by decreasing the level of body coloration exhibited and turning off the eyebar signal, thus matching female coloration these males can school with the females and hide (Korzan et al., 2008; Parikh et al., 2006). Still other fish species, such as various salmonids, have behavioral and color changes, dictated by genetics, to cope with social stress by modifying release of stress hormones (Backström et al., 2015a; Backström et al., 2015b; Cruz and Brown, 2007; Freitas et al., 2014; Höglund et al., 2000; Höglund et al., 2002; Kittilsen et al., 2009; Kittilsen et al., 2012; Lin et al., 2009; Miyai et al., 2011; O'Connor et al., 1999; Volpato et al., 2003). Change in coloration for male *A. carolinensis* lizards also signals to stop aggression received (Korzan et al., 2021). Males turn from bright green to dark brown and this strategy is very powerful in stopping the aggressive behavior from the dominant animal (Greenberg et al., 1984a; Summers et al., 2005a). A more proactive behavioral coping response is escape (Arendt et al., 2012b; Dishman et al., 1997; Gallon, 1972; Horner et al., 1997; Maier, 1990; Summers et al., 2017). In the Stress Alternatives Model (SAM; see section 3.2.) (Robertson et al., 2015), designed to allow for escape during socially aggressive interactions, this behavior can be rapidly learned (Smith et al., 2014), and links this proactive behavior with reduced stress reactivity, because anxiety and stress-reducing drugs (CRF₁ antagonist, Orx₂ agonist) and behavior (running wheel) increase the likelihood of escape, and decrease the latency to escape (Smith et al., 2016; Staton et al., 2018). Conversely, anxiogenic stress-inducing drugs (α₂ antagonist, Orx₁ agonist) limit escape behavior (Pang et al., 2021; Smith et al., 2016; Yaeger et al., 2020).

1.3. Stability of social rank

One attribute of social hierarchies that is not often investigated is the stability of rank relationships among members of a group. The advantages of living in groups, such as predator avoidance, improved foraging and feeding opportunities, improved reproductive opportunities, and improved social decision-making (King and Cowlshaw, 2007; Rubenstein, 1978) provides positive pressure for the formation social hierarchies. Rank relationships must be stable enough to benefit the entire group. Stable status relationships decrease social stress, and result in more advantageous living conditions for all individuals. For the cichlid *A. burtoni*, stability in rank relationships is maintained through extreme levels of aggression (over 70 percent of each minute is dedicated to agonistic behavior for the first 3 h) as the sun rises, aggression is resumed by the previous day's dominant males (Ferno, 1987; Korzan and Fernald, 2005). Other species rely, in part, on memory, such as male *A. carolinensis* lizards (Forster et al., 2005; Korzan and Summers, 2007; Summers et al., 2005a). Thus, stability in rank relationships can be perpetuated by multiple mechanisms, that include repeated aggression, chronobiology, and memory, and likely other mechanisms as well (such as health and fitness). As status is not permanent, despite the advantages

of stability, change in rank is probably also regulated by multiple factors.

1.4. Flexibility of rank relationships

Behavioral flexibility appears to be important attribute of coping (Coppens et al., 2010) with stressful, including socially stressful conditions. Social rank produces distinctively proactive and passive phenotypes (Korzan and Summers, 2007; Øverli et al., 2007), which differ in behavioral flexibility. Proactive dominant individuals are less flexible, more rigid, behaviorally (Bolhuis et al., 2004; Coppens et al., 2010; Johansen et al., 2012; Ruiz-Gomez Mde et al., 2011), because social dominance confers advantages of course, but also because the resumption of subordinate status is more costly for former dominant individuals (Laredo et al., 2015) whose prior status marks them as a continuing threat. Despite that, rank relationships are by nature changeable, and dominant individuals are fungible. Of course, for a social system to work optimally there needs to be an appropriate amount of opportunity for individuals to increase their rank and thereby improve their overall fitness. Therefore, it is important to note that the effect of social defeat on flexibility is also determined by sex (Laredo et al., 2015). Many examples of large and long lived mammals follow an age related rank, such that social status increases with age (Pelletier and Festa-Bianchet, 2006), up to a point (Cote and Festa-Bianchet, 2001). As fitness and vigor increase, so does the possibility of elevated rank, but as health declines with age, there is an increase in rank flexibility. Simply put, the young and the old have much less opportunity to become dominant compared to animals in their prime years. Thus, health and fitness, are important factors for rank stability. In the case of *A. burtoni* dominant males spend a majority of their calories defending and maintaining their territory. As a result, they do not grow as fast and lose weight compared to the subordinate males. Subordinate individuals grow larger, and eventually displace dominant males (Korzan et al., 2008). Individual dominant fish will cycle through weight loss and gain, becoming dominant and subordinate many times during their lives. Dominant rainbow trout have been demonstrated to switch behavioral profiles following traumatic environmental stressors, and lose rank status (Ruiz-Gomez Mde et al., 2008). However, the offspring of the original dominant fish were also dominant, suggesting that genetic or epigenetic attributes are modifiable, at least temporarily, by environmental conditions. In male *A. carolinensis* lizards, individually recognized social rank carries the advantage of decreased aggression from opponents for slightly more than a week, but is lost after 10 days (Forster et al., 2005; Korzan and Summers, 2007; Summers et al., 2005a). These examples suggest that rank relationships are modifiable, by individual health, environmental, stress-related, genetic, and memory-associated mechanisms, regulated by distinctive changes in the nervous system (Burmeister et al., 2005, 2007).

1.4.1. Inflexibility associated with social dominance

Attaining dominant social rank can be energetically and/or socially expensive. In some species of lizards, where tail loss is common to avoid predators, it often comes with loss of social status, for males and females (Fox et al., 1990). Some evidence has suggested that dominant individuals are more susceptible to stress, and thus more vulnerable to depression. However, this link appears to be more closely related to loss of social rank and its resources, than to dominant status specifically (Larrieu and Sandi, 2018). For a number of species, there is no return from the loss of dominant rank status. In the insectivorous dasyurid marsupial *Antechinus stuartii*, dominant males exhibit intensive aggressive social interactions during territorial invasions throughout mating season. They respond with dramatic stress reactivity, and die shortly thereafter, unless they are removed from territorial interactions (Barker et al., 1978; Barnett, 1973; Bradley et al., 1980; Braithwaite, 1974). Dominant male lions have been recorded on video as suffering fatal injuries during battles to maintain status and females in the pride,

though no systematic study has determined whether this fate is common. It seems likely that in many species, loss of dominant status has dramatic consequences, which may result in mortality.

2. Social stress and aggression

2.1. Social stress is uncontrollable stress

It is important to consider that individuals involved in development of social rank relationships cannot control the amount of stress that develops from those social interactions (Summers et al., 2005a). First, the individuals involved are initially naïve to each other. Additionally, although this changes with time and experience, there is a period during which neither animal can control the reaction of their opponent. Thus, this social stress is not only uncontrollable before rank relationships are established; but is also unpredictable throughout the encounter. Even while the development of social roles during the aggressive interaction improves controllability and on average increases predictability; motivation, previous experience, and erratic foray opportunities result in unpredictable attacks from either individual.

2.1.1. The importance of unpredictable and uncontrollable stressors

Uncontrollable stressors have dramatically different effects on neuroendocrine and behavioral responsiveness from those stressors that can be controlled, resulting in potentiation of fearful responses and conditioning (Baratta et al., 2007; Der-Avakian et al., 2007; Hammack et al., 2002; Rozeske et al., 2011). The effects of uncontrollable stressors can, however, be modified behaviorally, or by the possibility of escape (Baratta et al., 2007; Greenwood et al., 2005). Despite the unpredictable and uncontrollable nature of the initial interaction, enhanced dominant or subordinate behavioral phenotypes occur as individuals of each phenotype acquire behavioral characteristics that are adaptive for continued survival. In a natural setting, subordinate animals may often control the stressor, simply by leaving. Escape is a dramatically useful behavioral option, that reduces stressful potential of interactions substantially (Carpenter et al., 2009; Smith et al., 2014; Staton et al., 2018; Summers et al., 2017). The result is that continued social interaction in captivity is an extremely stressful condition in the short term for animals that will become either dominant or subordinate, and a chronically stressful situation for subordinate individuals (Summers, 2002). Subordinate individuals denied an opportunity to evade dominant opponents may suffer from a deadly chronic stress syndrome, conditioned defeat (Huhman et al., 2003), major depression (Bjorkqvist, 2001), or its animal equivalent (Van Kampen et al., 2002). Social subordination is in some ways not unlike the uncontrollable stress paradigm that produces learned helplessness, with similar effects on stress-related systems in the brain (Fernandez Macedo et al., 2013; Greenwood et al., 2003; Greenwood and Fleshner, 2008; Hammack et al., 2002, 2012; Maier and Watkins, 2005; Petty et al., 1993, 1994a, 1994b, 1997; Vollmayr et al., 2001).

2.2. Non-aggressive behavior

Behaviors that are not explicitly aggressive play an important role in social rank attainment. There are numerous types of behavioral displays and competitive behaviors that provide evidence of aggressive intent, without being an attack, a chase, a bite, hitting, clawing, or displacement. Baring teeth and/or snarling certainly suggest aggressive motivation, but do not cause bodily injury. Psychological damage may be as potent as physical wounds for establishing dominant social rank or high hierarchical status, and emotional injury can yield long-lasting stress responsibility (Summers and Winberg, 2006). Additionally, behaviors that do not portend actual aggression, including competitive behaviors and those that signal rapid stress responsiveness, may create the needed emotional effect to produce dominant status (Andrews and Summers, 1996; Korzan et al., 2006; Summers and Greenberg, 1994; Summers

et al., 1997).

Directly aggressive acts, such as biting, hitting, or clawing produces both emotional and physical wounds, but are also very costly to the individual seeking elevated social status, because they cannot be delivered without close contact (Blanchard et al., 1975, 1985; Robertson et al., 2015; Sapolsky, 1987; Smith et al., 2014; Takahashi and Blanchard, 1982). For this reason, it is evolutionarily adaptive to include displays suggesting aggressive intent in addition to actual aggression (DeCourcy and Jenssen, 1994; Greenberg, 1977; Jenssen et al., 2005). Some of these behaviors clearly signal heightened aggressive motivation, such as bearing teeth and snarling, and other aggressive displays require experience and memory to be effective, including raised hackles in feline and canine species, and extended dewlap and pushup displays in lizards. Interestingly, dewlap/pushup displays can signal both aggressive intent and mating (DeCourcy and Jenssen, 1994; Greenberg, 1977; Jenssen et al., 2005), and courtship is competitive behavior.

Competitive behavior includes any actions that focus on access to resources rather than producing physical harm. Lions protecting food resources at a kill, engage in aggressive looking behavior. Often baring teeth, roaring, and other displays are primarily associated with energy management, but also confer elevated social rank, if the displays are successful. Some behavioral displays, such as lizard dewlap extensions and pushups, are similar for aggression and reproduction. Perhaps the reason that is that both aggression and reproduction also serve to enhance social status.

Memory associated with individual recognition and identification of status is mediated by specific limbic regions of the brain, such as hippocampus and amygdala. Not surprisingly, this type of memory that is more potent with regard to social rank than other signal stimuli (Korzan et al., 2007), and is controlled by regions of the brain that are also critical for territoriality via spatial and recognition memory (Eacret et al., 2019), fear learning (Pang et al., 2021; Yaeger et al., 2020), and stress responsiveness (Smith et al., 2016).

Celerity of the stress response appears to be a critical component of elevated social rank (Korzan et al., 2006; Korzan and Summers, 2007; Sapolsky, 1982, 1983, 1988, 1989; Summers and Greenberg, 1994; Summers et al., 2005a). This relationship between rapid and brief stress neurochemical responses, but also behavioral responses, and elevated social status is evident in a wide range of vertebrates, from fish (Øverli et al., 1999), to lizards (Korzan et al., 2006; Korzan and Summers, 2007; Summers, 2001; Summers et al., 2005c), and to primates (Sapolsky, 1982). For example, in the lizard *A. carolinensis*, rapid stress responsiveness (Summers, 2001; Summers et al., 2003) in dominant males is combined with other types of rapid behavioral responses. Feeding and courtship behaviors in dominant males follow with a much shorter latency after presentation of food or females (Korzan et al., 2006; Korzan and Summers, 2007). This relationship between increased social stress and reduced food intake is common across vertebrates, is affected by food quality and sex (Cruz and Brown, 2007; Cubitt et al., 2008; Foerster et al., 2011; Riedel et al., 2020; Ruiz-Gomez Mde et al., 2008; Ruiz-Gomez Mde et al., 2011), and is also present in salmon that emerge earlier after spawning (Vaz-Serrano et al., 2011). In this way, non-aggressive behaviors occur in a similar temporal profile in dominant individuals as aggression, and neuroendocrine stress responses (Korzan and Summers, 2007).

The behavior of individuals that eventually become subordinate can be very aggressive, at least initially (Summers, 2002; Summers et al., 2005c). However, as the establishment of social rank progresses, defensive behaviors begin to predominate (Blanchard et al., 1990a, 1990b, 1992, 1993b, 1997, 1998a, 1998b, 1998c, 2001d, 2003, 2008; Blanchard and Blanchard, 1989a; Griebel et al., 1996; Takahashi and Blanchard, 1982; Wall et al., 2004b; Yang et al., 2006). These defensive behaviors signal the time when status phenotype adjustment can begin (Summers, 2002). It is important to note that chronic stress alters defensive burying behavior (Bhatnagar et al., 2003), so stress can influence behavioral phenotypes. In the SAM (see section 3.2.), there are

two distinctive behavior phenotypes in subordinate animals, Escape and Stay (remaining with the dominant opponent), suggesting that even in socially defeated animals there are pro-active and passive coping styles (Carpenter and Summers, 2009; Robertson et al., 2015; Smith et al., 2014, 2016; Staton et al., 2018; Summers et al., 2017; Yaeger et al., 2020).

2.3. What stimulates aggression

While aggression and behavioral displays that threaten aggression are central to the establishment of social rank relationships, the specific behavioral qualities that provoke or trigger aggression are not so well known. Aggression is displayed for a variety of reasons, and in healthy animals reserved for the last option to resolve competition for a resource (Blanchard and Blanchard, 2003). Simple presence of a competitor within territorial bounds may be sufficient unless rank-related accommodations have developed during the establishment of hierarchies. Aggressive postures provoke agonistic responses, but the definition of an aggressive posture is different for each species, and presumably for different conditions. Some signals triggering aggression are less ambiguous. In the lizard *A. carolinensis* the presence of an appropriately (green) colored moving object is not enough to stimulate aggression (Yang et al., 2001), but an active green male (without eyespots) stimulates aggressive response, whether the image is virtual (mirror or video) or real (Korzan et al., 2021). The presence of a blackened eyespot (produced by activation of β_2 -adrenoreceptors) (Goldman and Hadley, 1969; Goldman and Hadley, 1970; Hadley and Goldman, 1969) (in the skin behind the eye) (Summers and Greenberg, 1994) inhibits aggression (Korzan et al., 2000a, 2000b, 2002; Korzan and Summers, 2004), as does brown skin on the lizard, but for different reasons. Brown skin indicates submission, and rapid eyespot development indicates an opponent of dominant status. Aggression is unwarranted if the fight is already over (brown skin), or if it is one that is not likely to be winnable (faster black eyespot on opponent) (Korzan et al., 2021). Aggression begets aggression, as does previous experience (Korzan et al., 2021; Schwartz et al., 2013; Yang et al., 2001; Yang and Wilczynski, 2002). These effects produce measurable changes in the neural and hormonal systems involved in aggression and stress (Korzan et al., 2021). The neurocircuitry producing aggressive behavior (Fig. 1) will serve to suggest what triggers may be associated with aggressive attack.

The central node for inducing agonistic behavior (Fig. 1) is a region of the ventral hypothalamus extending from ventrolateral subdivisions of anterior hypothalamus (LAH) to the ventromedial hypothalamus (vlVMH) (Ferris et al., 2008; Kruk et al., 1979, 1998; Lin et al., 2011; Takahashi et al., 2012). Also known as the attack area, this region receives widespread input from other elements of aggression neurocircuitry, including medial amygdala, bed nucleus of the stria terminalis, lateral septum, prefrontal cortex, and brainstem monoamine nuclei such as raphé and locus ceruleus (David et al., 2004; Delville et al., 2000; Greenberg et al., 1984b; McLott et al., 2013) that modify aggressive output (Grimes and Melloni, 2002; Haller et al., 2006; Miczek et al., 2007; Summers and Winberg, 2006; Takahashi et al., 2012). The principal aggression-related neurons of ventral hypothalamus are glutamatergic with projections to periaqueductal gray which sends efferents to motor neurons producing aggressive behavior (Fig. 1). These glutamatergic neurons are modulated directly or indirectly by vasopressinergic, dopaminergic, serotonergic, and GABAergic neurons (Ferris et al., 1997; Maxson and Canastar, 2003; Miczek et al., 2001) that produce nuanced and contextually appropriate behavior for the social and environmental conditions that exist at any given moment (Robertson et al., 2015). Aggressive behavior is stimulated by glutamatergic inputs from lateral septum and medial amygdala as well as by dopaminergic afferents and local AVP; it is inhibited by serotonergic afferents and local GABA (Ferris et al., 1997) (Fig. 1). Optogenetic stimulation of the vlVMH causes male mice to attack male or female mice and even inanimate objects (Lin et al., 2011). Arginine vasopressin (AVP) in

ventral hypothalamus has been associated with aggressive behavior in numerous vertebrate species including humans (Albers, 2012; Coccaro et al., 1998; Godwin and Thompson, 2012; Goodson, 2013; Heinrichs and Domes, 2008; Luppino et al., 2014). Increased expression or pharmacological activation of the V_{1A} AVP receptor in LAH of the monogamous prairie vole facilitates aggression that is reversed by V_{1A} and V_{1B} antagonists (Gobrogge et al., 2009). Intranasal AVP delivery to human males increased bias toward aggressive response to ambiguous social stimuli, stimulated agonistic facial motor patterns, and increased anxiety (Thompson et al., 2006). Androgens (Yang and Wilczynski, 2002) and corticosterone (Yang and Wilczynski, 2003) have similarly been demonstrated to stimulate aggression.

Aggression stimulated in response to interaction between conspecifics occurs when an individual seeks to reinforce superior social standing, or in the case of unfamiliar conspecifics to establishing status. Critically for this kind of interaction, pyramidal neurons in the hippocampal CA2 region is the location of stored social standing memories (Leroy et al., 2018), and provides the functional link to allow aggression, since recognition actively inhibits aggression after social hierarchy is established (Korzan et al., 2007). A circuit connection between CA2 and lateral septum is selectively enhanced immediately before an attack. Vasopressinergic (AVP) enhancement of CA2 activation of lateral septum results in disinhibition of vlVMH to trigger attack (Leroy et al., 2018). As the hippocampus is also a critical component of the stress neurocircuitry, this direct link establishes active regulatory interaction between stress and aggression (Summers and Winberg, 2006).

2.4. Role of aggression in social dominance

In animal and human aggression, status and territorial control of resources provide motivations for aggressive challenge between conspecifics (Blanchard and Blanchard, 2003). More often than not, aggression is the direct precedent for social dominance, perhaps because there are long-term consequences for the outcomes of aggressive interactions (Koolhaas et al., 1997b; Meerlo et al., 1997). These types of social aggression bouts reinforce status on subordinate individuals. In addition, successful aggressive establishment of rank makes it easier for females to identify the current dominant male, who is also more successful reproductively (Sapolsky, 1982; Summers, 1995; Summers et al., 1995, 1997). This is especially true for species that use similar behaviors for aggression and attracting mates. For instance, female lizards near the aggressive arena, capable of viewing head bobs by an interacting male would recognize that individual as dominant in the area. Similarly, for other males close enough to notice the head bobs, the display also reinforces status and territorial ownership on more subordinate males.

2.4.1. Winner and loser effects

A single experience of a major stressor like social defeat has long-term consequences, such that this experience acts to sensitize the defeated animal to subsequent stressors (Koolhaas et al., 1997b). Conversely, winning a competitive social interaction typically has benefits for future interactions (Dugatkin and Druen, 2004). This is most obvious when opponents are of equal size and condition. Evolutionarily, the costs are reduced when the performance of stereotypical or ritual behavioral movements become associated with aggression, and thereby limit actual aggression. Individual variation in performance may help produce contest wins, and also aid in recognition of specific individuals and their dominant status. As it is likely that these specific differences will be repeated during subsequent interactions, the behavioral effect is magnified, promoting a winner effect. In poikilotherms, like trout and lizards, the temporal aspect of these ritual behaviors seems to be a key characteristic. Individuals that initiate a variety of aggressive and non-aggressive behaviors most quickly are much more likely to win agonistic contests than individuals that are slower to react (Korzan et al., 2006; Korzan and Summers, 2007; Øverli et al., 2004a, 2007; Summers, 2001; Summers et al., 2005a). Individual recognition is thought to be a

stabilizing factor for social hierarchies, such that recognition of opponents overrides winner and loser effects (Dugatkin and Earley, 2004). In the lizard *A. carolinensis*, memory of previous opponents, and therefore winner and loser effects have a 10 day limit (Forster et al., 2005), indicating that social recognition and memory modify aggression.

3. Social stress and decision-making

As stressful social interactions progress, opportunities to adaptively alter behavior occur repeatedly across time, and frequently allow for decision-making (Robertson et al., 2015; Smith et al., 2014). Many decision-making opportunities are associated with environmental, predatory, and social stressors, as stressful events are often the catalyst for making decisions regarding behavioral modifications necessary to temporarily adapt to novel stressful conditions. As stressful social interactions are unpredictable and uncontrollable (Summers et al., 2005a), social interactions produce numerous opportunities for this type of behavioral adaptation.

3.1. Inter-related stress and decision-making neural circuitries

Emotional and executive neurocircuitry elements, including amygdala and extended amygdala (such as bed nucleus of the stria terminalis – BNST), prefrontal cortex (PFC), cingulate cortex, nucleus accumbens, ventral tegmental area, hippocampus, paraventricular hypothalamus, are often refunctioned for numerous related purposes, such as stress, reward salience, and decision-making (Bechara et al., 2003; de Visser et al., 2010, 2011a, 2011b). These reciprocally connected regions, form circuits responsible for stress responsiveness and coping strategies, resilience or susceptibility to anxious or despair-related behavior, seeking and abusing reward (Fig. 1), producing adaptive social responses such as submissive, aggressive, or escape behaviors, and the critical decision-making that is associated with adopting these behaviors (Arendt et al., 2012a; Carpenter and Summers, 2009; Feder et al., 2009; Krishnan et al., 2007; Smith et al., 2014, 2016; Summers et al., 2017; Tanaka et al., 2012). As decision-making processes involve neurocircuitry that includes emotional and executive brain regions, they are necessarily influenced by stressors (Bechara et al., 1999; Brand et al., 2007; de Visser et al., 2010, 2011a, 2011b), and these executive functions cannot proceed exclusive of stress inputs. While the decision-making circuitry includes the amygdala, orbitofrontal cortex, anterior cingulate, dorsolateral prefrontal cortex, ventral and dorsal striatum (Bechara et al., 2003; de Visser et al., 2011a; Koot et al., 2012), these regions also regulate affect and emotional responses via specialized pro-stress and anti-stress microcircuits, which are differentiated by intracellular genetic biomarkers that are unique to the specific microcircuits (Kim et al., 2016; Yaeger et al., 2020). This suggests that stress-related circuitry that includes the amygdala (Fig. 1) is important for social decision-making (Arendt et al., 2012a; Carpenter and Summers, 2009; Smith et al., 2014; Summers et al., 2020; Yaeger et al., 2020).

3.2. Evolutionary importance of decision-making during stress

While submissive, aggressive, or avoidance responses are considered elements of anxious and depressive disorders in human populations, they are also adaptive reactions to environmental and social stressors, and thereby important factors in decisions regarding social and environmental conditions. A simple social stress decision making paradigm is the Stress Alternatives Model (SAM) which aggressively apposes two size-distinct individuals in an oval interaction arena with escape tunnels at the polar ends of the apparatus (Robertson et al., 2015; Smith et al., 2014, 2016; Staton et al., 2018). This model allows for comparison of decision-making strategies and neural function across evolutionarily disparate species, such as rainbow trout and mice (Carpenter and Summers, 2009; Robertson et al., 2015; Smith et al., 2014; Summers

et al., 2017). The SAM is a Go – No Go decision paradigm in which the choice is made between 1. Egress from or 2. remaining with a significantly larger competitor during socially aggressive interactions. Interestingly, experiments using the SAM paradigm in rainbow trout and mice show identical ratios (~50/50) of Escape (egress via apical escape route) and Stay (remaining) phenotypes. Similarly, both fish and rodents require stress-reduction (via CRF₁ receptor antagonist antalarmin for example) to allow stress-sensitive Stay animals to reverse behavioral phenotype and become Escape animals (Carpenter and Summers, 2009; Smith et al., 2016; Staton et al., 2018; Summers et al., 2017). Stress-promoting drugs (such as the α_2 adrenoreceptor antagonist yohimbine), produce behavioral reversal in animals that Escape, to become Stay phenotype individuals, or slow escape latency (Smith et al., 2016). Thus, some qualities of stress responsiveness dramatically influence decision-making, and are evolutionarily conserved.

3.3. How decision-making during stress determines social rank

The two behavioral phenotypes (Escape and Stay) expressed in SAM social interactions give evidence of multiple stress-coping strategies employed during social interaction, which result in active and passive responses (Koolhaas et al., 1999, 2007, 2011; Øverli et al., 2007). Additionally, Escape animals show resilience to stress (such as in the Social Interaction/Preference test) and Stay animals exhibit vulnerability. While both groups respond to fear conditioning, the plasma corticosterone response to fear conditioning is much greater in Stay animals (Carpenter and Summers, 2009; Smith et al., 2016). Animals that demonstrate more rapid proactive responses to aggression, feeding, courtship, social displays, and stress recovery are much more likely to become dominant individuals (FitzGerald and Kedny, 1987; Höglund et al., 2001; Höglund et al., 2005; Koolhaas et al., 1999; Korzan et al., 2006; Korzan and Summers, 2007; Korzan et al., 2021; Lailvaux et al., 2004; Øverli et al., 1998; Øverli et al., 2004a; Ruiz-Gomez Mde et al., 2008; Summers and Greenberg, 1994; Summers et al., 2005b; Summers et al., 2005c; Winberg et al., 1993), and social dominance has been demonstrated to be positively correlated with cognitive ability (Boogert et al., 2006). Rapid stress responsiveness of neurotransmitter (such as serotonin and dopamine activity) and stress hormone responses (corticosterone or cortisol) are key elements promoting dominant status in individuals that contend for that position (Korzan and Summers, 2007; Ling et al., 2009; Øverli et al., 1999; Summers and Greenberg, 1994; Summers et al., 1998, 2003, 2005c; Summers and Winberg, 2006). The neural signaling systems that are influenced by proactive Escape phenotype include brain-derived neurotrophic factor (BDNF), cannabinoids (Cb₂ receptors), corticotropin releasing factor (CRF; CRF₁ receptors), dopamine (DA), neuropeptide S (NPS), norepinephrine (NE, adrenergic receptors), orexin (Orx; Orx₁ and Orx₂ receptors), and serotonin (5-HT) (Carpenter and Summers, 2009; Robertson et al., 2015, 2017; Smith et al., 2014, 2016; Staton et al., 2018; Summers et al., 2017, 2020; Yaeger et al., 2020), suggesting that these changes may accrue to the advantage of individuals in the process of seeking dominant social status.

3.4. Established social rank modifies decision-making

For humans, primates and many other social species social rank clearly alters day to day choices of behavioral output (Abbott et al., 2003; Gong and Sanfey, 2017; Sapolsky, 1991, 1992). Lizards and fish that establish social hierarchies also exhibit modified behavior based on rank relevant to a conspecific (Carpenter and Summers, 2009; Korzan and Summers, 2007; Summers et al., 2017). In male *A. carolinensis* with established ranks, behavioral output is changed if they are reintroduced to previous opponents (Forster et al., 2005; Korzan et al., 2007; Korzan and Summers, 2007; Summers et al., 2005a). Individuals remember each other, and they modify responses based on rank. Among territorial males of the teleost fish *A. burtoni*, neighbors watched and learned from

agonistic social interactions, and then modified their behavioral output based on their rank compared to animals they observed (Burmeister et al., 2005; Butler et al., 2018; Carpenter et al., 2014; Grosenick et al., 2007; Korzan et al., 2008; Maruska et al., 2013; Maruska and Fernald, 2018). Successful defeat of an opponent, promotes dominance over other males defeated by the opponent, which they attack immediately.

4. Celerity of the stress response

In the early work on social rank relationships, when stress or stress hormones were considered, the typical result reported was that subordinate individuals exhibited elevated plasma corticosteroid concentrations, but dominant individuals did not. At the time, most reports suggested that the timeline of steroid secretion lasted over a period of hours or longer, and most researchers never examined the possibility that adrenal or inter-renal glucocorticoid responses could be promulgated and extinguished much faster. As circadian control of corticosterone rhythmicity began to be investigated, it was discovered that daily patterns of secretion could be modified by relatively minor environmental stressors (such as humidity) (Summers and Norman, 1988), but also that the normal pattern of secretion and concentration levels in plasma and brain were pulsatile (Droste et al., 2008; Lightman et al., 2000). These ultradian rhythms had a periodicity of about an hour, the frequency of which increased during stress (Lightman, 2008). Pulses were created through a transient refractory period, inhibiting HPA axis functioning following secretion, and the pulse/refractory period may be altered by changes in genetic expression, reproductive status, pain, and other life experiences (Lightman et al., 2002). This opened the door to the idea that steroid stress responses could be promoted and extinguished much faster than previously expected. Social stress stimulated by aggression between rats resulted in very rapid increases in plasma corticosterone (Schuurman, 1980). Adrenal medullary responses were always known to be fast, on the order of seconds. In the lizard *Anolis carolinensis*, a small patch of skin just behind the eye, which densely concentrated β_2 -adrenergic receptors, and responded primarily to norepinephrine (NE) (Korzan et al., 2002), responded more rapidly in male lizards that became dominant (Summers and Greenberg, 1994). Studies in trout, and in these lizards, also demonstrated that very rapid increases in plasma corticosteroid and brain monoaminergic activity also occurred in dominant individuals (Øverli et al., 1999; Summers, 2001; Summers et al., 2003, 2005c). The data suggested that the celerity, or rapidity, of the stress response may have some functional meaning.

4.1. Functional value of rapid stress responsiveness

As experimental evidence mounted it became clear that dominant individuals had a significantly different stress response than subordinate individuals (Summers, 2002; Summers and Winberg, 2006). Under social stress conditions, which are considered to be the most intense type of stressors (Koolhaas et al., 1997a), dominant individuals have more rapid onset of behavioral (Korzan et al., 2006; Øverli et al., 2004a), catecholaminergic hormonal/sympathetic (Summers and Greenberg, 1994), corticosteroid hormonal (Øverli et al., 1999; Summers, 2002; Summers et al., 2003, 2005c), serotonergic, norepinephrine and dopaminergic neurotransmitter (Ling et al., 2010; Summers et al., 1998, 2003, 2005b; Summers, 2001; Summers and Winberg, 2006; Watt et al., 2007) responses. Subordinate individuals respond more slowly for these important signaling matters, but more importantly, these systems also recover more slowly in subordinate animals as well (Øverli et al., 1999; Summers, 2001; Summers et al., 2003, 2005c). The behavioral responses in individuals with more rapid onset and recovery of stress responsiveness are also more proactive, and those with slower onset and recovery exhibit behaviors that are more passive (Korzan et al., 2006; Summers et al., 2005a). Taken together, the data suggest that the rapid onset and recovery of stress responsiveness provides functional advantages that

promote advancement in social rank (Korzan et al., 2006; Korzan and Summers, 2007; Øverli et al., 1999, 2004a; Sapolsky, 1982; Summers and Greenberg, 1994; Summers et al., 2005b; Summers and Winberg, 2006).

4.2. Stress responsiveness modifies the plasticity of social rank

Accumulated data from the SAM paradigm demonstrates that the basic decision-making process associated with the dichotomous choice (Escape or Stay) during stressful social interactions produces relatively stable behavioral phenotypes with distinctly active (Escape) or passive (Stay) manifestations (Carpenter and Summers, 2009; Robertson et al., 2015; Smith et al., 2014, 2016; Staton et al., 2018; Yaeger et al., 2020). In other models, proactive and passive stress coping strategies are often related to dominant and subordinate rank status, respectively (Korzan and Summers, 2007; Øverli et al., 2007). These phenotypes also demonstrate stress resilience for Escape animals, and stress vulnerability in Stay individuals (Staton et al., 2018; Yaeger et al., 2020). Taken together, these accumulated relationships suggest that rapid turnover of the stress response, that is, quick onset and brief duration for stress responses in dominant, active, and resilient individuals leads to the ability to more quickly return to feeding, courtship, territorial protection, and other resource acquisition behaviors after stressful encounters or conditions (Korzan et al., 2006). It is important to note that while individuals may be resilient to stress, that may not confer improved learning, especially under stressful conditions, as vulnerable Stay animals evince stronger cued and contextual fear conditioning than resilient Escape individuals (Carpenter and Summers, 2009; Smith et al., 2014; Summers et al., 2017), and other types of learning may be stronger in passive stress coping individuals or in active stress coping animals (Bolhuis et al., 2004; Coppens et al., 2010; Dalley et al., 2004). What seems evident is that critical learning events are specifically tuned to both behavioral phenotypes, and that this learning plays an important role in the phenotypic development (Pang et al., 2021), which includes social rank assessments and self-assessments. Finally, it is clear that Escape and Stay phenotypes are plastic, depending on stress-related neurotransmitter and neuropeptide actions, with more stress-sensitive individuals adopting Stay phenotypes, which are reversible by anxiolytic drugs or neuropeptides (Carpenter and Summers, 2009; Robertson et al., 2017; Smith et al., 2014, 2016; Staton et al., 2018; Summers et al., 2017, 2020; Yaeger et al., 2020). As dominant status is by definition a temporary state, we argue that stress responsiveness, as well as the learning that is associated with resilient or vulnerable phenotypes, are the primary instigators behind change in social rank.

5. Role of sign stimuli in social rank

5.1. Social signals modify behavior

Sign stimuli are typically visible behavioral releasers, under evolutionary pressure to be honest signals. Sign stimuli that relay important information about an individual's momentary physiological state are especially powerful descriptions of condition during resource competition (Blount and McGraw, 2008; Summers, 2001; Summers et al., 2005a; Svensson and Wong, 2011). In salmonid and other fish, skin and eye color, often relative to background color, have been demonstrated to influence the aggressive behavior of opponents in territorial encounters (Kelley et al., 2016; O'Connor et al., 1999; Svensson and Wong, 2011). Male *A. carolinensis* lizards that become dominant express eyespot signals first and maintain it longer than their opponents (Korzan et al., 2006; Korzan and Summers, 2007). This work suggests that latency to aggressive behaviors, as well as eyespot signals, are reliable predictors of future social status for individual male *A. carolinensis*. This is also true for the teleost species *A. burtoni* eyebar signal (Muske and Fernald, 1987a, 1987b). In this species the individual animal has control over the eyebar signal and expresses it while conducting aggressive behaviors,

and each fish can see when its own signal is on or off. The signal is such an honest cue that if the nerve controlling the activation of the eyebar is severed on one side of the fish but not the other, the displaying dominant male will only show that side of his body while conducting aggressive behaviors (Muske and Fernald, 1987a, 1987b).

6. Memory

6.1. Social recognition, individual recognition

The critical elements in social interactions that involve territoriality or social rank include spatial memory, object recognition (Eacret et al., 2019), social recognition (Choleris et al., 2009; Ferguson et al., 2002; Kendrick, 2006; Young, 2002), and individual recognition (Couzin et al., 2002; Ferguson et al., 2002; Gheusi et al., 1994; Potts and Lewis, 2016; Tibbetts and Dale, 2007; Wiley, 2013). Recognizing spatial relationships is generally considered hippocampal function (Falkenberg et al., 1992; Morris et al., 2006; Sandi et al., 2005), in which “space cells” indicate location of the self, at least for mammals (Eichenbaum et al., 1999). Critically, spatial memory plays a vital role in social defeat (Eacret et al., 2019) and territorial ownership (Araya-Salas et al., 2018). However, even among invertebrate and non-mammalian vertebrates, species can also recognize territorial limits (Araya-Salas et al., 2018; Greenfield et al., 1989) and intrusions (Jaeger et al., 2005), social groups (De Luca et al., 2014), individuals (Gherardi et al., 2012; Karavanich and Atema, 1998), and individual rank (Aquiloni et al., 2012; Forster et al., 2005; Karavanich and Atema, 1998; Korzan et al., 2007). Importantly, this kind of individual and rank identification potentially influences neuroendocrine stress responses to social challenge (Ling et al., 2010).

6.2. The primacy of memory over other determinants of social rank

For animals forming social hierarchies it is advantageous to be able to identify specific individuals with whom they have interacted (Ferguson et al., 2002). Unknown conspecific competitors present unpredictable and uncontrollable behavioral responses (Summers et al., 2005a). For both *A. carolinensis* and *A. burtoni*, individuals immediately recognize previous combatants, their status, and adjust behavior accordingly (Fernald, 2017; Forster et al., 2005; Korzan et al., 2007; Maruska and Fernald, 2018; Summers et al., 2005a), making use of evolutionarily conserved types of behavior and neural regulatory systems (Butler et al., 2018). In *A. carolinensis*, eyespot celerity determines initial rank, but rematches adhere to rank memory, in spite of eyespot color (Korzan et al., 2007). For this lizard, memory is the most important component of social rank establishment for similarly sized animals, and for rank stability. In mammals, three sensory systems may be involved in determining whether a conspecific and emotional valence are remembered: auditory (of vocalizations), olfaction, and vision (Arakawa et al., 2008; Blanchard et al., 1993a; Brennan and Kendrick, 2006; Miczek et al., 1995; Parr et al., 2000). In mice and rats individual recognition (Choleris et al., 2009; Gheusi et al., 1994, 1997) of two conspecifics and their social rank results in reduced investigation (Thor et al., 1982), and no challenge (or dramatically reduced aggression), but dominant maintenance aggression occurs (Blanchard and Blanchard, 1977; Blanchard et al., 1988a, 1988b, 2001c). Thus, memory of social rank can have dramatic benefits for both dominant and subordinate individuals.

6.3. The importance of the duration of memories

If memory of a social opponent or interaction has the greatest impact on social rank, then the duration of those memories is also of prime importance for maintaining social rank. Memories, like rank, are not permanent. For example, orexin signaling during social defeat conditioning decreases subsequent social interaction and recognition performance and memory with increased anxious behavior (Eacret et al., 2019). In male green anoles (*A. carolinensis*) the memory of previous

opponents operates to modify aggressive behavior for over a week, but then is lost after ten days of separation (Forster et al., 2005; Korzan et al., 2007; Summers et al., 2005a) and they react as if completely unaware of the opponent's identity and status. Mammals on the other hand maintain memories of previous opponents much longer, and in the case of humans for the rest of their lives. Recently an important neural location for representation and actuation of agonistic social memories in mice has been identified (Leroy et al., 2018). Pyramidal cells in the CA2 region of the hippocampus are important for social memories; and stimulation of CA2 to lateral septum pathway, promotes social aggression. As CA2 type pyramidal cells are broadly conserved evolutionarily (Meyer et al., 2004), as is septum, it may be that this circuit is widely active in many social rank relationships.

The previous example of *A. carolinensis* males exhibiting approximately ten days of opponent identity and rank memory (Forster et al., 2005; Korzan et al., 2007; Summers et al., 2005a) is suggestive of the dynamism of rank relationships. Re-pairing opponents after 10 days resulted in robust agonistic encounters, with winners and losers equally successful. As winner effects are expunged, any individual has the possibility of achieving dominant status, the temporary nature of social rank is obvious for this species. In fact, memory of opponent identity and status after some period is maladaptive. We wonder if similar timelines for rank extinction exist for other lizards, birds, or mammals. If so, memories of previous opponents may be more influential for second interactions than sign stimuli or other important factors, like weight, size, or fitness, but may not be for third or fourth interactions. Therefore, the number of days after the initial interaction, may be critical information for social rank assessments.

7. Synergistic social stimuli

Cumulative effects of sensory social stimuli on interactions establishing rank relationships may be additive or synergistic (Korzan et al., 2006; Korzan and Summers, 2007; Summers et al., 2005a). Our work on the lizard *A. carolinensis* suggests that there are at least four stimuli that affect the rank outcomes of social interactions, including: 1. Acting Aggressively, 2. Viewing Aggressive Acts by an opponent, 3. Viewing Darkened (black) Eyespots on an opponent, and 4. Viewing Darkened (brown) Skin on an opponent (Korzan et al., 2021). Of these, the first three increase stress responsiveness, and the latter reduces it. Critically, a fifth element dramatically enhances the synergistic effect on stress responsiveness and rank outcome, and that is memory of the opponent (Korzan et al., 2007). The synergistic effect is measurable in plasma NE secretion and hippocampal serotonergic activity (5-HIAA/5-HT) and suggests a dramatic increase in emotional activation (Korzan et al., 2021). Differing degrees of emotional activation associated with different intensities of social interaction (such as dominant-subordinate interaction, dominant-dominant confrontation, or social defeat) in rats can produce relatively stronger shifts of autonomic balance toward sympathetic dominance (Sgoifo et al., 1999).

7.1. Motivation to respond to stimuli

Stressful conditions drastically change outcomes of interactions with social and physical environments (Pang et al., 2021). Response to an opportunity in the physical environment, such as using an escape route to an unknown destination and resources, elevates the level of anxiety in an individual, but that apprehension becomes dramatically larger when social stress is added to the context (Carpenter and Summers, 2009; Smith et al., 2014). The Stress Alternatives model (SAM) examines this type of Go/No Go decision making in the context of aggressive social interaction (Carpenter and Summers, 2009; Robertson et al., 2015; Smith et al., 2014, 2016). Elevated social stress levels associated with a patrolling dominant individual reduces the likelihood of using an escape route to avoid that individual (Smith et al., 2016; Summers et al., 2017).

8. Predicting social rank

8.1. *Anolis carolinensis* Predicting social rank

The most obvious and successful way to predict the social rank of two combatants is size, larger and thus stronger individuals will win a majority of contests (Wright et al., 2019). However, regardless of size, other factors come into play; such as physical condition and species specific signals (Wright et al., 2019). In *A. carolinensis* a portion of skin post-orbital to each eye darkens during social interactions (Goldman and Hadley, 1969, 1970; Hadley and Goldman, 1969; Summers and Greenberg, 1994). As stated above, latency to eyespot darkening during an aggressive interaction between male *A. carolinensis* accurately predicts the social status of each combatant (Höglund et al., 2005; Korzan et al., 2006; Larson and Summers, 2001; Summers and Greenberg, 1994). In addition, previous experiments suggested that the first to display aggression will become dominant in dyadic interactions (Korzan and Summers, 2004; Korzan et al., 2006; Summers, 2002). However, these are characteristics of paired males while engaged in aggressive contest for social dominance. It is perhaps more remarkable that predicting social dominance is possible using behavioral motivation for experiences unrelated to social aggression. Males that become dominant court females considerably sooner, than those that become subordinate (Korzan et al., 2006). Similarly, lizards and fish that become dominant respond to food sooner (Korzan et al., 2006; Øverli et al., 2004a). These are striking relationships for seemingly unrelated events. It is advantageous to forecast social dominance, because assessing rank without aggression reduces the cost of social interaction (Summers et al., 2005b).

9. Conclusions

We suggest that the evolution of social status is inextricably linked to the evolution of stress. To understand this relationship completely, there remains a need for a greater examination of rank relationships in a diverse array of animals (Keifer and Summers, 2016). Specifically, there is a need for methods for greater examination of species-specific, stress-related, anxious and depressive behaviors, using ecologically and ethologically relevant tests that also examine motivation, decision-making, learning and memory (Carpenter and Summers, 2009; Morrison et al., 2015; Smith et al., 2014; Summers et al., 2017; Yaeger et al., 2020). As stress responsiveness is ubiquitous, the basic elements that produce social rank relationships are universally present, and widespread among both male and female animals. Social rank relationships are molded by aggressive interactions, which are inherently stressful. The neurocircuitries associated with stress, aggression, reward, and decision-making interact directly and indirectly to produce these outcomes. It seems likely that the balance of regulatory elements in pro- and anti-stress neurocircuitries results in rapid but brief stress responses, that are advantages to social dominance. These systems further produce, in coordination with reward and aggression circuitries, rapid adaptive responding during opportunities that arise to acquire food, mates, perch sites, territorial space, shelter and other resources. This rapid acquisition of resources and aggressive postures produces dominant individuals, who temporarily have distinct fitness advantages.

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CRedit authorship contribution statement

Wayne J. Korzan: Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Cliff H. Summers:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors have no conflicts of interest to disclose.

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References

- Abbott, D.H., Keverne, E.B., Bercovitch, F.B., Shively, C.A., Mendoza, S.P., Saltzman, W., Snowdon, C.T., Ziegler, T.E., Banjevic, M., Garland Jr., T., Sapolsky, R.M., 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Horm. Behav.* 43, 67–82.
- Albeck, D.S., McKittrick, C.R., Blanchard, D.C., Blanchard, R.J., Nikulina, J., McEwen, B. S., Sakai, R.R., 1997. Chronic social stress alters levels of corticotropin-releasing factor and arginine vasopressin mRNA in rat brain. *J. Neurosci.* 17, 4895–4903.
- Albers, H.E., 2012. The regulation of social recognition, social communication and aggression: vasopressin in the social behavior neural network. *Horm. Behav.* 61, 283–292.
- Amat, J., Paul, E., Zarza, C., Watkins, L.R., Maier, S.F., 2006. Previous experience with behavioral control over stress blocks the behavioral and dorsal raphe nucleus activating effects of later uncontrollable stress: role of the ventral medial prefrontal cortex. *J. Neurosci.* 26, 13264–13272.
- Andrews, T.J., Summers, C.H., 1996. Aggression, and the acquisition and function of social dominance in female *Anolis carolinensis*. *Behaviour*, 133, 1265–1279.
- Anisman, H., Sklar, L.S., 1981. Social housing conditions influence escape deficits produced by uncontrollable stress: assessment of the contribution of norepinephrine. *Behav. Neural. Biol.* 32, 406–427.
- Aquiloni, L., Goncalves, V., Inghilesi, A.F., Gherardi, F., 2012. Who's what? Prompt recognition of social status in crayfish. *Behav. Ecol. Sociobiol.* 66, 785–790.
- Arakawa, H., Arakawa, K., Blanchard, D.C., Blanchard, R.J., 2008. A new test paradigm for social recognition evidenced by urinary scent marking behavior in C57BL/6J mice. *Behav. Brain Res.* 190, 97–104.
- Araya-Salas, M., Gonzalez-Gomez, P., Wojczulanis-Jakubas, K., Lopez 3rd, V., Wright, T. F., 2018. Spatial memory is as important as weapon and body size for territorial ownership in a lekking hummingbird. *Sci. Rep.* 8, 2001.
- Arendt, D.H., Smith, J.P., Bastida, C.C., Prasad, M.S., Oliver, K.D., Eyster, K.M., Summers, T.R., Delville, Y., Summers, C.H., 2012a. Contrasting hippocampal and amygdalar expression of genes related to neural plasticity during escape from social aggression. *Physiol. Behav.* 107, 670–679.
- Arendt, D.H., Smith, J.P., Bastida, C.C., Prasad, M.S., Oliver, K.D., Eyster, K.M., Summers, T.R., Delville, Y., Summers, C.H., 2012b. Contrasting hippocampal and amygdalar expression of genes related to neural plasticity during escape from social aggression. *Physiol. Behav.* 107, 670–679.
- Backström, T., Winberg, S., 2009. Arginine-vasotocin influence on aggressive behavior and dominance in rainbow trout. *Physiol. Behav.* 96, 470–475.

- Backström, T., Pettersson, A., Johansson, V., Winberg, S., 2011a. CRF and urotensin I effects on aggression and anxiety-like behavior in rainbow trout. *J. Exp. Biol.* 214, 907–914.
- Backström, T., Schjolden, J., Øverli, Ø., Thornqvist, P.O., Winberg, S., 2011b. Stress effects on AVT and CRF systems in two strains of rainbow trout (*Oncorhynchus mykiss*) divergent in stress responsiveness. *Horm. Behav.* 59, 180–186.
- Backström, T., Winberg, S., 2013. Central corticotropin releasing factor and social stress. *Front. Neurosci.* 7, 117.
- Backström, T., Heynen, M., Brannas, E., Nilsson, J., Magnhagen, C., 2015a. Dominance and stress signalling of carotenoid pigmentation in Arctic charr (*Salvelinus alpinus*): lateralization effects? *Physiol. Behav.* 138, 52–57.
- Backström, T., Heynen, M., Brannas, E., Nilsson, J., Winberg, S., Magnhagen, C., 2015b. Social stress effects on pigmentation and monoamines in Arctic charr. *Behav. Brain Res.* 291, 103–107.
- Backström, T., Winberg, S., 2017. Serotonin coordinates responses to social stress-what we can learn from fish. *Front. Neurosci.* 11, 595.
- Bangasser, D.A., Valentino, R.J., 2012. Sex differences in molecular and cellular substrates of stress. *Cell. Mol. Neurobiol.* 32, 709–723.
- Bangasser, D.A., 2013. Sex differences in stress-related receptors: “micro” differences with “macro” implications for mood and anxiety disorders. *Biol. Sex Differ.* 4, 2.
- Baratta, M.V., Christianson, J.P., Gomez, D.M., Zarza, C.M., Amat, J., Masini, C.V., Watkins, L.R., Maier, S.F., 2007. Controllable versus uncontrollable stressors bidirectionally modulate conditioned but not innate fear. *Neuroscience* 146, 1495–1503.
- Barker, I.K., Beveridge, I., Bradley, A.J., Lee, A.K., 1978. Observations on spontaneous stress-related mortality among males of dasyurid marsupial *Antechinus stuartii* macleay. *Aust. J. Zool.* 26, 435–447.
- Barnett, J.L., 1973. A stress response in *Antechinus stuartii* (Macleay). *Aust. J. Zool.* 21, 501–513.
- Bechara, A., Damasio, H., Damasio, A.R., Lee, G.P., 1999. Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. *J. Neurosci.* 19, 5473–5481.
- Bechara, A., Damasio, H., Damasio, A.R., 2003. Role of the amygdala in decision-making. *Ann. N. Y. Acad. Sci.* 985, 356–369.
- Benus, R.F., Bohus, B., Koolhaas, J.M., van Oortmerssen, G.A., 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia* 47, 1008–1019.
- Berton, O., McClung, C.A., Dileone, R.J., Krishnan, V., Renthal, W., Russo, S.J., Graham, D., Tsankova, N.M., Bolanos, C.A., Rios, M., Monteggia, L.M., Self, D.W., Nestler, E.J., 2006. Essential role of BDNF in the mesolimbic dopamine pathway in social defeat stress. *Science* 311, 864–868.
- Bhatnagar, S., Huber, R., Lazar, E., Pych, L., Vining, C., 2003. Chronic stress alters behavior in the conditioned defensive burying test: role of the posterior paraventricular thalamus. *Pharmacol., Biochem. Behav.* 76, 343–349.
- Bhatnagar, S., Vining, C., Denski, K., 2004. Regulation of chronic stress-induced changes in hypothalamic-pituitary-adrenal activity by the basolateral amygdala. *Ann. N. Y. Acad. Sci.* 1032, 315–319.
- Bingham, B., McFadden, K., Zhang, X., Bhatnagar, S., Beck, S., Valentino, R., 2011. Early adolescence as a critical window during which social stress distinctly alters behavior and brain norepinephrine activity. *Neuropsychopharmacology* 36, 896–909.
- Bjorkqvist, K., 2001. Social defeat as a stressor in humans. *Physiol. Behav.* 73, 435–442.
- Blanchard, C., Blanchard, R., Fellous, J.M., Guimaraes, F.S., Irwin, W., Ledoux, J.E., McGaugh, J.L., Rosen, J.B., Schenberg, L.C., Volchan, E., Da Cunha, C., 2001a. The brain decade in debate: III. Neurobiology of emotion. *Braz. J. Med. Biol. Res.* 34, 283–293.
- Blanchard, D.C., Flannelly, K., Hori, K., Blanchard, R.J., Hall, J., 1987a. Ethanol effects on female aggression vary with opponent size and time within session. *Pharmacol. Biochem. Behav.* 27, 645–648.
- Blanchard, D.C., Blanchard, R.J., 1990. Behavioral correlates of chronic dominance-subordination relationships of male rats in a seminatural situation. *Neurosci. Biobehav. Rev.* 14, 455–462.
- Blanchard, D.C., Blanchard, R.J., Tom, P., Rodgers, R.J., 1990a. Diazepam changes risk assessment in an anxiety/defense test battery. *Psychopharmacology (Berlin)* 101, 511–518.
- Blanchard, D.C., Shepherd, J.K., Rodgers, R.J., Blanchard, R.J., 1992. Evidence for differential effects of 8-OH-DPAT on male and female rats in the Anxiety/Defense Test Battery. *Psychopharmacology (Berlin)* 106, 531–539.
- Blanchard, D.C., Spencer, R.L., Weiss, S.M., Blanchard, R.J., McEwen, B., Sakai, R.R., 1995. Visible burrow system as a model of chronic social stress: behavioral and neuroendocrine correlates. *Psychoneuroendocrinology* 20, 117–134.
- Blanchard, D.C., Griebel, G., Rodgers, R.J., Blanchard, R.J., 1998a. Benzodiazepine and serotonergic modulation of antipredator and conspecific defense. *Neurosci. Biobehav. Rev.* 22, 597–612.
- Blanchard, D.C., Blanchard, R.J., 2003. What can animal aggression research tell us about human aggression? *Horm. Behav.* 44, 171–177.
- Blanchard, D.C., Griebel, G., Blanchard, R.J., 2003. The Mouse Defense Test Battery: pharmacological and behavioral assays for anxiety and panic. *Eur. J. Pharmacol.* 463, 97–116.
- Blanchard, D.C., Blanchard, R.J., Rosen, J., 2008. Olfaction and defense. *Neurosci. Biobehav. Rev.* 32, 1207–1208.
- Blanchard, D.C., Summers, C.H., Blanchard, R.J., 2013. The role of behavior in translational models for psychopathology: functionality and dysfunctional behaviors. *Neurosci. Biobehav. Rev.* 37, 1567–1577.
- Blanchard, R.J., Fukunaga, K., Blanchard, D.C., Kelley, M.J., 1975. Conspecific aggression in the laboratory rat. *J. Comp. Physiol. Psychol.* 89, 1204–1209.
- Blanchard, R.J., Blanchard, D.C., 1977. Aggressive behavior in the rat. *Behav. Biol.* 21, 197–224.
- Blanchard, R.J., Blanchard, D.C., Flannelly, K.J., 1985. Social stress, mortality and aggression in colonies and burrowing habitats. *Behav. Process.* 11, 209–213.
- Blanchard, R.J., Hori, K., Blanchard, D.C., Hall, J., 1987b. Ethanol effects on aggression of rats selected for different levels of aggressiveness. *Pharmacol. Biochem. Behav.* 27, 641–644.
- Blanchard, R.J., Flannelly, K.J., Blanchard, D.C., 1988a. Life-span studies of dominance and aggression in established colonies of laboratory rats. *Physiol. Behav.* 43, 1–7.
- Blanchard, R.J., Hori, K., Tom, P., Blanchard, D.C., 1988b. Social-dominance and individual aggressiveness. *Aggress. Behav.* 14, 195–203.
- Blanchard, R.J., Blanchard, D.C., 1989a. Attack and defense in rodents as ethoexperimental models for the study of emotion. *Prog. Neuro-Psychopharmacol. Biol. Psychiatry* 13 (Suppl. 1), S3–S14.
- Blanchard, R.J., Blanchard, D.C., 1989b. Antipredator defensive behaviors in a visible burrow system. *J. Comp. Psychol.* 103, 70–82.
- Blanchard, R.J., Blanchard, D.C., Weiss, S.M., 1990b. Ethanol effects in an anxiety/defense test battery. *Alcohol* 7, 375–381.
- Blanchard, R.J., Yudko, E.B., Blanchard, D.C., Taukulis, H.K., 1993a. High-frequency (35–70 kHz) ultrasonic vocalizations in rats confronted with anesthetized conspecifics: effects of gepirone, ethanol, and diazepam. *Pharmacol. Biochem. Behav.* 44, 313–319.
- Blanchard, R.J., Yudko, E.B., Rodgers, R.J., Blanchard, D.C., 1993b. Defense system psychopharmacology: an ethological approach to the pharmacology of fear and anxiety. *Behav. Brain Res.* 58, 155–165.
- Blanchard, R.J., Griebel, G., Henrie, J.A., Blanchard, D.C., 1997. Differentiation of anxiolytic and panicolytic drugs by effects on rat and mouse defense test batteries. *Neurosci. Biobehav. Rev.* 21, 783–789.
- Blanchard, R.J., Hebert, M.A., Dulloog, L., Kaawaloa, N., Nishimura, O., Blanchard, D.C., 1998b. Acute cocaine effects on stereotype and defense: an ethoexperimental approach. *Neurosci. Biobehav. Rev.* 23, 179–188.
- Blanchard, R.J., Hebert, M.A., Ferrari, P., Palanza, P., Figueira, R., Blanchard, D.C., Parmigiani, S., 1998c. Defensive behaviors in wild and laboratory (Swiss) mice: the mouse defense test battery. *Physiol. Behav.* 65, 201–209.
- Blanchard, R.J., Dulloog, L., Markham, C., Nishimura, O., Nikulina, C.J., Jun, A., Han, C., Blanchard, D.C., 2001b. Sexual and aggressive interactions in a visible burrow system with provisioned burrows. *Physiol. Behav.* 72, 245–254.
- Blanchard, R.J., McKittrick, C.R., Blanchard, D.C., 2001c. Animal models of social stress: effects on behavior and brain neurochemical systems. *Physiol. Behav.* 73, 261–271.
- Blanchard, R.J., Yudko, E., Dulloog, L., Blanchard, D.C., 2001d. Defense changes in stress nonresponsive subordinate males in a visible burrow system. *Physiol. Behav.* 72, 635–642.
- Blanchard, R.J., Griebel, G., Farrokhi, C., Markham, C., Yang, M., Blanchard, D.C., 2005. AVP V1b selective antagonist SSR149415 blocks aggressive behaviors in hamsters. *Pharmacol. Biochem. Behav.* 80, 189–194.
- Blount, J.D., McGraw, K.J., 2008. Signal Functions of Carotenoid Colouration. Carotenoids, Basel, Switzerland. Birkhauser.
- Bolhuis, J.E., Schouten, W.G., de Leeuw, J.A., Schrama, J.W., Wiegant, V.M., 2004. Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behav. Brain Res.* 152, 351–360.
- Boogert, N.J., Reader, S.M., Laland, K.N., 2006. The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.* 72, 1229–1239.
- Bradley, A.J., McDonald, I.R., Lee, A.K., 1980. Stress and mortality in a small marsupial (*Antechinus stuartii*, Macleay). *Gen. Comp. Endocrinol.* 40, 188–200.
- Braithwaite, R.W., 1974. Behavioral-changes associated with population cycle of *Antechinus-stuartii* (marsupialia). *Aust. J. Zool.* 22, 45–62.
- Brand, M., Grabenhorst, F., Starcke, K., Vandekerckhove, M.M., Markowitsch, H.J., 2007. Role of the amygdala in decisions under ambiguity and decisions under risk: evidence from patients with Urbach-Wiethe disease. *Neuropsychologia* 45, 1305–1317.
- Brennan, P.A., Kendrick, K.M., 2006. Mammalian social odours: attraction and individual recognition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 361, 2061–2078.
- Burleson, C.A., Pedersen, R.W., Seddighi, S., DeBusk, L.E., Burghardt, G.M., Cooper, M.A., 2016. Social play in juvenile hamsters alters dendritic morphology in the medial prefrontal cortex and attenuates effects of social stress in adulthood. *Behav. Neurosci.* 130, 437–447.
- Burmeister, S.S., Jarvis, E.D., Fernald, R.D., 2005. Rapid behavioral and genomic responses to social opportunity. *PLoS Biol.* 3, e363.
- Burmeister, S.S., Kailasanath, V., Fernald, R.D., 2007. Social dominance regulates androgen and estrogen receptor gene expression. *Horm. Behav.* 51, 164–170.
- Butler, J.M., Whitlow, S.M., Roberts, D.A., Maruska, K.P., 2018. Neural and behavioural correlates of repeated social defeat. *Sci. Rep.* 8, 6818.
- Butler, J.M., Whitlow, S.M., Rogers, L.S., Putland, R.L., Mensinger, A.F., Maruska, K.P., 2019. Reproductive state-dependent plasticity in the visual system of an African cichlid fish. *Horm. Behav.* 114, 104539.
- Caldwell, H.K., Aulino, E.A., Rodriguez, K.M., Witchev, S.K., Yaw, A.M., 2017. Social context, stress, neuropsychiatric disorders, and the vasopressin 1b receptor. *Front. Neurosci.* 11, 567.
- Carpenter, R.E., Korzan, W.J., Bockholt, C., Watt, M.J., Forster, G.L., Renner, K.J., Summers, C.H., 2009. Corticotropin releasing factor influences aggression and monoamines: modulation of attacks and retreats. *Neuroscience* 158, 412–425.
- Carpenter, R.E., Summers, C.H., 2009. Learning strategies during fear conditioning. *Neurobiol. Learn. Mem.* 91, 415–423.
- Carpenter, R.E., Maruska, K.P., Becker, L., Fernald, R.D., 2014. Social opportunity rapidly regulates expression of CRF and CRF receptors in the brain during social ascent of a teleost fish, *Astatotilapia burtoni*. *PLoS One* 9, e96632.

- Carrillo, M., Ricci, L.A., Melloni, R.H., 2011. Glutamate-vasopressin interactions and the neurobiology of anabolic steroid-induced offensive aggression. *Neuroscience* 185, 85–96.
- Chajjale, N.N., Curtis, A.L., Wood, S.K., Zhang, X.Y., Bhatnagar, S., Reyes, B.A., Van Bockstaele, E.J., Valentino, R.J., 2013. Social stress engages opioid regulation of locus coeruleus norepinephrine neurons and induces a state of cellular and physical opiate dependence. *Neuropsychopharmacology* 38, 1833–1843.
- Chappell, M.A., Zuk, M., Johnsen, T.S., 1999. Aerobic performance does not affect social rank in female Red Jungle Fowl. *Funct. Ecol.* 13, 163–168.
- Choleris, E., Clipperton-Allen, A.E., Phan, A., Kavaliers, M., 2009. Neuroendocrinology of social information processing in rats and mice. *Front. Neuroendocrinol.* 30, 442–459.
- Christian, J.J., 1968. The potential role of the adrenal cortex as affected by social rank and population density on experimental epidemics. *Am. J. Epidemiol.* 87, 255–264.
- Christianson, J.P., Thompson, B.M., Watkins, L.R., Maier, S.F., 2009. Medial prefrontal cortical activation modulates the impact of controllable and uncontrollable stressor exposure on a social exploration test of anxiety in the rat. *Stress* 12, 445–450.
- Christianson, J.P., Jennings, J.H., Ragole, T., Flyer, J.G., Benison, A.M., Barth, D.S., Watkins, L.R., Maier, S.F., 2011. Safety signals mitigate the consequences of uncontrollable stress via a circuit involving the sensory insular cortex and bed nucleus of the stria terminalis. *Biol. Psychiatr.* 70, 458–464.
- Chung, K.K., Martinez, M., Herbert, J., 1999. Central serotonin depletion modulates the behavioural, endocrine and physiological responses to repeated social stress and subsequent c-fos expression in the brains of male rats. *Neuroscience* 92, 613–625.
- Coccaro, E.F., Kavoussi, R.J., Hauger, R.L., Cooper, T.B., Ferris, C.F., 1998. Cerebrospinal fluid vasopressin levels: correlates with aggression and serotonin function in personality-disordered subjects. *Arch. Gen. Psychiatr.* 55, 708–714.
- Cooper, M.A., Grober, M.S., Nicholas, C.R., Huhman, K.L., 2009. Aggressive encounters alter the activation of serotonergic neurons and the expression of 5-HT1A mRNA in the hamster dorsal raphe nucleus. *Neuroscience* 161, 680–690.
- Coppens, C.M., de Boer, S.F., Koolhaas, J.M., 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 4021–4028.
- Cote, S.D., Festa-Bianchet, M., 2001. Reproductive success in female mountain goats: the influence of age and social rank. *Anim. Behav.* 62, 173–181.
- Couzin, I.D., Krause, J., James, R., Ruxton, G.D., Franks, N.R., 2002. Collective memory and spatial sorting in animal groups. *J. Theor. Biol.* 218, 1–11.
- Crúz, E.M.V., Brown, C.L., 2007. The influence of social status on the rate of growth, eye color pattern and Insulin-like Growth Factor-I gene expression in Nile tilapia, *Oreochromis niloticus*. *Horm. Behav.* 51, 611–619.
- Cubitt, K.F., Winberg, S., Huntingford, F.A., Kadri, S., Crampton, V.O., Øverli, Ø., 2008. Social hierarchies, growth and brain serotonin metabolism in Atlantic salmon (*Salmo salar*) kept under commercial rearing conditions. *Physiol. Behav.*
- Dalley, J.W., Cardinal, R.N., Robbins, T.W., 2004. Prefrontal executive and cognitive functions in rodents: neural and neurochemical substrates. *Neurosci. Biobehav. Rev.* 28, 771–784.
- David, J.T., Cervantes, M.C., Trosky, K.A., Salinas, J.A., Delville, Y., 2004. A neural network underlying individual differences in emotion and aggression in male golden hamsters. *Neuroscience* 126, 567–578.
- de Almeida, R.M., Benini, Q., Betat, J.S., Hipolide, D.C., Miczek, K.A., Svensson, A.I., 2008. Heightened aggression after chronic flunitrazepam in male rats: potential links to cortical and caudate-putamen-binding sites. *Psychopharmacology (Berlin)* 197, 309–318.
- de Boer, S.F., van der Vegt, B.J., Koolhaas, J.M., 2003. Individual variation in aggression of feral rodent strains: a standard for the genetics of aggression and violence? *Behav. Genet.* 33, 485–501.
- de Boer, S.F., Koolhaas, J.M., 2005. 5-HT 1A and 5-HT 1B receptor agonists and aggression: a pharmacological challenge of the serotonin deficiency hypothesis. *Eur. J. Pharmacol.* 526, 125–139.
- De Goeij, D.C., Dijkstra, H., Tilders, F.J., 1992. Chronic psychosocial stress enhances vasopressin, but not corticotropin-releasing factor, in the external zone of the median eminence of male rats: relationship to subordinate status. *Endocrinology* 131, 847–853.
- De Luca, G., Mariani, P., MacKenzie, B.R., Marsili, M., 2014. Fishing out collective memory of migratory schools. *J. R. Soc. Interface* 11.
- de Visser, L., van der Knaap, L.J., van de Loo, A.J., van der Weerd, C.M., Ohl, F., van den Bos, R., 2010. Trait anxiety affects decision-making differently in healthy men and women: towards gender-specific endophenotypes of anxiety. *Neuropsychologia* 48, 1598–1606.
- de Visser, L., Baars, A.M., Lavrijsen, M., van der Weerd, C.M., van den Bos, R., 2011a. Decision-making performance is related to levels of anxiety and differential recruitment of prefrontal areas in male rats. *Neuroscience* 184, 97–106.
- de Visser, L., Baars, A.M., van 't Klooster, J., van den Bos, R., 2011b. Transient inactivation of the medial prefrontal cortex affects both anxiety and decision-making in male wistar rats. *Front. Neurosci.* 5, 102.
- DeCourcy, K.R., Jessen, T.A., 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Animal Behaviour*, 47, 251–262.
- Delville, Y., Mansour, K.M., Ferris, C.F., 1996a. Testosterone facilitates aggression by modulating vasopressin receptors in the hypothalamus. *Physiol. Behav.* 60, 25–29.
- Delville, Y., Mansour, K.M., Ferris, C.F., 1996b. Serotonin blocks vasopressin-facilitated offensive aggression: interactions within the ventrolateral hypothalamus of golden hamsters. *Physiol. Behav.* 59, 813–816.
- Delville, Y., De Vries, G.J., Ferris, C.F., 2000. Neural connections of the anterior hypothalamus and agonistic behavior in golden hamsters. *Brain Behav. Evol.* 55, 53–76.
- Der-Avakian, A., Bland, S.T., Rozeske, R.R., Tamblyn, J.P., Hutchinson, M.R., Watkins, L.R., Maier, S.F., 2007. The effects of a single exposure to uncontrollable stress on the subsequent conditioned place preference responses to oxytocin, cocaine, and ethanol in rats. *Psychopharmacology (Berlin)* 191, 909–917.
- Dewan, A.K., Ramey, M.L., Tricas, T.C., 2011. Arginine vasotocin neuronal phenotypes, telencephalic fiber varicosities, and social behavior in butterflyfishes (Chaetodontidae): potential similarities to birds and mammals. *Horm. Behav.* 59, 56–66.
- Dewan, A.K., Tricas, T.C., 2011. Arginine vasotocin neuronal phenotypes and their relationship to aggressive behavior in the territorial monogamous multiband butterflyfish, *Chaetodon multicinctus*. *Brain Res.* 1401, 74–84.
- DiBattista, J.D., Anisman, H., Whitehead, M., Gilmour, K.M., 2005. The effects of cortisol administration on social status and brain monoaminergic activity in rainbow trout *Oncorhynchus mykiss*. *J. Exp. Biol.* 208, 2707–2718.
- Dinzburg, A.L., Chirkov, A.M., Chirkova, S.K., Voit, I.S., 1992. Stress-inducing behavioral changes and the functions of the neurohormonal systems in monkeys of different social ranks. *Biull. Eksp. Biol. Med.* 114, 457–459.
- Dishman, R.K., Renner, K.J., Youngstedt, S.D., Reigle, T.G., Bunnell, B.N., Burke, K.A., Yoo, H.S., Mougey, E.H., Meyerhoff, J.L., 1997. Activity wheel running reduces escape latency and alters brain monoamine levels after footshock. *Brain Res. Bull.* 42, 399–406.
- Dodman, N.H., Donnelly, R., Shuster, L., Mertens, P., Rand, W., Miczek, K., 1996. Use of fluoxetine to treat dominance aggression in dogs. *J. Am. Vet. Med. Assoc.* 209, 1585–1587.
- Doyon, C., Gilmour, K.M., Trudeau, V.L., Moon, T.W., 2003. Corticotropin-releasing factor and neuropeptide Y mRNA levels are elevated in the preoptic area of socially subordinate rainbow trout. *Gen. Comp. Endocrinol.* 133, 260–271.
- Droste, S.K., de Groote, L., Atkinson, H.C., Lightman, S.L., Reul, J.M., Linthorst, A.C., 2008. Corticosterone levels in the brain show a distinct ultradian rhythm but a delayed response to forced swim stress. *Endocrinology* 149, 3244–3253.
- Dugatkin, L.A., Druen, M., 2004. The social implications of winner and loser effects. *Proc. Biol. Sci.* 271, S488–S489.
- Dugatkin, L.A., Earler, R.L., 2004. Individual recognition, dominance hierarchies and winner and loser effects. *Proc. Biol. Sci.* 271, 1537–1540.
- Eacret, D., Grafe, L.A., Dobkin, J., Gotter, A.L., Renger, J.J., Winrow, C.J., Bhatnagar, S., 2019. Orexin signaling during social defeat stress influences subsequent social interaction behaviour and recognition memory. *Behav. Brain Res.* 356, 444–452.
- Eagle, A.L., Manning, C.E., Williams, E.S., Bastle, R.M., Gajewski, P.A., Garrison, A., Wirtz, A.J., Akguen, S., Brandel-Ankrapp, K., Endege, W., Boyce, F.M., Ohnishi, Y.N., Mazei-Robison, M., Maze, I., Neve, R.L., Robison, A.J., 2020. Circuit-specific hippocampal DeltaFosB underlies resilience to stress-induced social avoidance. *Nat. Commun.* 11, 4484.
- Eichenbaum, H., Dudchenko, P., Wood, E., Shapiro, M., Tanila, H., 1999. The hippocampus, memory, and place cells: is it spatial memory or a memory space? *Neuron* 23, 209–226.
- Eichenbaum, H., 2017. Prefrontal-hippocampal interactions in episodic memory. *Nat. Rev. Neurosci.* 18, 547–558.
- Ejike, C., Schreck, C.B., 1980. Stress and social hierarchy rank in coho salmon. *Trans. Am. Fish. Soc.* 109, 423–426.
- Elliott, E., Ezra-Nevo, G., Regev, L., Neufeld-Cohen, A., Chen, A., 2010. Resilience to social stress coincides with functional DNA methylation of the *Crf* gene in adult mice. *Nat. Neurosci.* 13, 1351–1353.
- Erhardt, A., Muller, M.B., Rodel, A., Welt, T., Ohl, F., Holsboer, F., Keck, M.E., 2009. Consequences of chronic social stress on behaviour and vasopressin gene expression in the PVN of DBA/20laHsd mice—influence of treatment with the CRHR1-antagonist R121919/NBI 30775. *J. Psychopharmacol.* 23, 31–39.
- Everts, H.G., De Ruiter, A.J., Koolhaas, J.M., 1997. Differential lateral septal vasopressin in wild-type rats: correlation with aggression. *Horm. Behav.* 31, 136–144.
- Falkenberg, T., Mohammed, A.K., Henriksson, B., Persson, H., Winblad, B., Lindfors, N., 1992. Increased expression of brain-derived neurotrophic factor mRNA in rat hippocampus is associated with improved spatial memory and enriched environment. *Neurosci. Lett.* 138, 153–156.
- Fanous, S., Terwilliger, E.F., Hammer Jr., R.P., Nikulina, E.M., 2011. Viral depletion of VTA BDNF in rats modulates social behavior, consequences of intermittent social defeat stress, and long-term weight regulation. *Neurosci. Lett.* 502, 192–196.
- Farrokhi, C., Blanchard, D.C., Griebel, G., Yang, M., Gonzales, C., Markham, C., Blanchard, R.J., 2004. Effects of the CRF1 antagonist SSR125543A on aggressive behaviors in hamsters. *Pharmacol. Biochem. Behav.* 77, 465–469.
- Feder, A., Nestler, E.J., Charney, D.S., 2009. Psychobiology and molecular genetics of resilience. *Nat. Rev. Neurosci.* 10, 446–457.
- Fekete, E.M., Zhao, Y., Li, C., Sabino, V., Vale, W.W., Zorrilla, E.P., 2009. Social defeat stress activates medial amygdala cells that express type 2 corticotropin-releasing factor receptor mRNA. *Neuroscience* 162, 5–13.
- Ferguson, J.N., Young, L.J., Insel, T.R., 2002. The neuroendocrine basis of social recognition. *Front. Neuroendocrinol.* 23, 200–224.
- Fernald, R.D., 2017. Cognitive skills and the evolution of social systems. *J. Exp. Biol.* 220, 103–113.
- Fernandez Macedo, G.V., Cladouchos, M.L., Sifonios, L., Cassanelli, P.M., Wikinski, S., 2013. Effects of fluoxetine on CRF and CRF1 expression in rats exposed to the learned helplessness paradigm. *Psychopharmacology (Berlin)* 225, 647–659.
- Ferno, A., 1987. Aggressive-behavior between territorial cichlids (*Astatotilapia burtoni*) in relation to rank and territorial stability. *Behaviour* 103, 241–258.
- Ferris, C.F., Potegal, M., 1988. Vasopressin receptor blockade in the anterior hypothalamus suppresses aggression in hamsters. *Physiol. Behav.* 44, 235–239.

- Ferris, C.F., Foote, K.B., Meltser, H.M., Plenby, M.G., Smith, K.L., Insel, T.R., 1992. Oxytocin in the amygdala facilitates maternal aggression. *Ann. N. Y. Acad. Sci.* 652, 456–457.
- Ferris, C.F., 1996. Serotonin diminishes aggression by suppressing the activity of the vasopressin system. *Ann. N. Y. Acad. Sci.* 794, 98–103.
- Ferris, C.F., Melloni Jr., R.H., Koppel, G., Perry, K.W., Fuller, R.W., Delville, Y., 1997. Vasopressin/serotonin interactions in the anterior hypothalamus control aggressive behavior in golden hamsters. *J. Neurosci.* 17, 4331–4340.
- Ferris, C.F., Stolberg, T., Kulkarni, P., Murugavel, M., Blanchard, R., Blanchard, D.C., Febo, M., Brevard, M., Simon, N.G., 2008. Imaging the neural circuitry and chemical control of aggressive motivation. *BMC Neurosci.* 9, 111.
- Festabianchet, M., 1991. The social system of bighorn Sheep - grouping patterns, kinship and female dominance rank. *Anim. Behav.* 42, 71–82.
- Fish, E.W., McKenzie-Quirk, S.D., Bannai, M., Miczek, K.A., 2008. 5-HT(1B) receptor inhibition of alcohol-heightened aggression in mice: comparison to drinking and running. *Psychopharmacology (Berlin)* 197, 145–156.
- FitzGerald, G.J., Kedny, G.I., 1987. Aggression, fighting and territoriality in sticklebacks: three different phenomena. *Biol. Behav.* 12, 186–195.
- Foerster, S., Cords, M., Monfort, S.L., 2011. Social behavior, foraging strategies, and fecal glucocorticoids in female blue monkeys (*Cercopithecus mitis*): potential fitness benefits of high rank in a forest guenon. *Am. J. Primatol.* 73, 870–882.
- Fokidis, H.B., Deviche, P., 2012. Brain arginine vasotocin immunoreactivity differs between urban and desert curve-billed thrashers, *Toxostoma curvirostre*: relationships with territoriality and stress physiology. *Brain Behav. Evol.* 79, 84–97.
- Forster, G.L., Watt, M.J., Korzan, W.J., Renner, K.J., Summers, C.H., 2005. Opponent recognition in male green anoles. *Anolis carolinensis Animal Behaviour* 69, 733–740.
- Fox, S.F., Heger, N.A., Delay, L.S., 1990. Social cost of tail loss in *Uta stansburiana* - lizard tails as status-signaling badges. *Anim. Behav.* 39, 549–554.
- Francis, R.C., Soma, K., Fernald, R.D., 1993. Social regulation of the brain-pituitary-gonadal axis. *Proc. Natl. Acad. Sci. U.S.A.* 90, 7794–7798.
- Freeman, E.W., Schulte, B.A., Brown, J.L., 2010. Investigating the impact of rank and ovarian activity on the social behavior of captive female african elephants. *Zoo Biol.* 29, 154–167.
- Freitas, R.H., Negrao, C.A., Felicio, A.K., Volpato, G.L., 2014. Eye darkening as a reliable, easy and inexpensive indicator of stress in fish. *Zoology (Jena)* 117, 179–184.
- Gallon, R.L., 1972. Effects of pretraining with fear and escape conditioning on shuttlebox avoidance acquisition by goldfish. *Psychol. Rep.* 31, 919–924.
- Gesto, M., Soengas, J.L., Rodriguez-Illamola, A., Miguez, J.M., 2014. Arginine vasotocin treatment induces a stress response and exerts a potent anorexigenic effect in rainbow trout, *Oncorhynchus mykiss*. *J. Neuroendocrinol.* 26, 89–99.
- Gherardi, F., Aquiloni, L., Tricarico, E., 2012. Revisiting social recognition systems in invertebrates. *Anim. Cognit.* 15, 745–762.
- Gheusi, G., Bluthé, R.M., Goodall, G., Dantzer, R., 1994. Social and individual recognition in rodents: methodological aspects and neurobiological bases. *Behav. Process.* 33, 59–87.
- Gheusi, G., Goodall, G., Dantzer, R., 1997. Individually distinctive odours represent individual conspecifics in rats. *Anim. Behav.* 53, 935–944.
- Gobrogge, K.L., Liu, Y., Young, L.J., Wang, Z., 2009. Anterior hypothalamic vasopressin regulates pair-bonding and drug-induced aggression in a monogamous rodent. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19144–19149.
- Godwin, J., Thompson, R., 2012. Nonapeptides and social behavior in fishes. *Horm. Behav.* 61, 230–238.
- Goldman-Rakic, P.S., Selemon, L.D., Schwartz, M.L., 1984. Dual pathways connecting the dorsolateral prefrontal cortex with the hippocampal formation and parahippocampal cortex in the rhesus monkey. *Neuroscience* 12, 719–743.
- Goldman, J.M., Hadley, M.E., 1969. *In vitro* demonstration of adrenergic receptors controlling melanophore responses of the lizard. *Anolis carolinensis Journal of Pharmacology and Experimental Therapeutics* 166, 1–7.
- Goldman, J.M., Hadley, M.E., 1970. Evidence for separate receptors for melanophore stimulating hormone and catecholamine regulation of cyclic AMP in the control of melanophore responses. *Br. J. Pharmacol.* 39, 160–166.
- Gong, X., Sanfey, A.G., 2017. Social rank and social cooperation: impact of social comparison processes on cooperative decision-making. *PLoS One* 12, e0175472.
- Gonzalez-Martinez, L.F., D'Aigle, J., Lee, S.M., Lee, H.J., Delville, Y., 2017. Social stress in early puberty has long-term impacts on impulsive action. *Behav. Neurosci.* 131, 249–261.
- Goodson, J.L., 2013. Deconstructing sociality, social evolution and relevant nonapeptide functions. *Psychoneuroendocrinology* 38, 465–478.
- Grafe, L.A., Geng, E., Corbett, B., Urban, K., Bhatnagar, S., 2019. Sex- and stress-dependent effects on dendritic morphology and spine densities in putative orexin neurons. *Neuroscience* 418, 266–278.
- Greenberg, N., 1977. A neuroethological study of display behavior in the lizard, *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). *Am. Zool.* 17, 191–201.
- Greenberg, N., Chen, T., Crews, D., 1984a. Social status, gonadal state, and the adrenal stress response in the lizard. *Anolis carolinensis Hormones and Behavior* 18, 1–11.
- Greenberg, N., Scott, M., Crews, D., 1984b. Role of the amygdala in the reproductive and aggressive behavior of the lizard. *Anolis carolinensis Physiol Behav* 32, 147–151.
- Greenfield, M.D., Alkaslassy, E., Wang, G.Y., Shelly, T.E., 1989. Long-term-memory in territorial grasshoppers. *Experientia* 45, 775–777.
- Greenwood, B.N., Foley, T.E., Day, H.E., Campisi, J., Hammack, S.H., Campeau, S., Maier, S.F., Fleshner, M., 2003. Free-wheel running prevents learned helplessness/behavioral depression: role of dorsal raphe serotonergic neurons. *J. Neurosci.* 23, 2889–2898.
- Greenwood, B.N., Foley, T.E., Burhans, D., Maier, S.F., Fleshner, M., 2005. The consequences of uncontrollable stress are sensitive to duration of prior wheel running. *Brain Res.* 1033, 164–178.
- Greenwood, B.N., Fleshner, M., 2008. Exercise, learned helplessness, and the stress-resistant brain. *NeuroMolecular Med.* 10, 81–98.
- Griebel, G., Blanchard, D.C., Jung, A., Masuda, C.K., Blanchard, R.J., 1995. 5-HT1A agonists modulate mouse antipredator defensive behavior differently from the 5-HT2A antagonist pirenperone. *Pharmacol. Biochem. Behav.* 51, 235–244.
- Griebel, G., Blanchard, D.C., Blanchard, R.J., 1996. Evidence that the behaviors in the Mouse Defense Test Battery relate to different emotional states: a factor analytic study. *Physiol. Behav.* 60, 1255–1260.
- Grimes, J.M., Melloni, R.H., 2002. Serotonin modulates offensive attack in adolescent anabolic steroid-treated hamsters. *Pharmacol., Biochem. Behav.* 73, 713–721.
- Grimes, J.M., Melloni Jr., R.H., 2005. Serotonin-1B receptor activity and expression modulate the aggression-stimulating effects of adolescent anabolic steroid exposure in hamsters. *Behav. Neurosci.* 119, 1184–1194.
- Grimes, J.M., Ricci, L.A., Melloni Jr., R.H., 2006. Plasticity in anterior hypothalamic vasopressin correlates with aggression during anabolic-androgenic steroid withdrawal in hamsters. *Behav. Neurosci.* 120, 115–124.
- Grosenick, L., Clement, T.S., Fernald, R.D., 2007. Fish can infer social rank by observation alone. *Nature* 445, 429–432.
- Hadley, M.E., Goldman, J.M., 1969. Physiological color changes in reptiles. *Am. Zool.* 9, 489–504.
- Haller, J., Toth, M., Halasz, J., De Boer, S.F., 2006. Patterns of violent aggression-induced brain c-fos expression in male mice selected for aggressiveness. *Physiol. Behav.* 88, 173–182.
- Hammack, S.E., Richey, K.J., Schmid, M.J., LoPresti, M.L., Watkins, L.R., Maier, S.F., 2002. The role of corticotropin-releasing hormone in the dorsal raphe nucleus in mediating the behavioral consequences of uncontrollable stress. *J. Neurosci.* 22, 1020–1026.
- Hammack, S.E., Cooper, M.A., Lezak, K.R., 2012. Overlapping neurobiology of learned helplessness and conditioned defeat: implications for PTSD and mood disorders. *Neuropharmacology* 62, 565–575.
- Hare, B.D., Shinohara, R., Liu, R.J., Pothula, S., DiLeone, R.J., Duman, R.S., 2019. Optogenetic stimulation of medial prefrontal cortex Drd1 neurons produces rapid and long-lasting antidepressant effects. *Nat. Commun.* 10, 223.
- Harmon, A.C., Huhman, K.L., Moore, T.O., Albers, H.E., 2002. Oxytocin inhibits aggression in female Syrian hamsters. *J. Neuroendocrinol.* 14, 963–969.
- Harrison, R.J., Connor, D.F., Nowak, C., Melloni Jr., R.H., 2000a. Chronic low-dose cocaine treatment during adolescence facilitates aggression in hamsters. *Physiol. Behav.* 69, 555–562.
- Harrison, R.J., Connor, D.F., Nowak, C., Nash, K., Melloni Jr., R.H., 2000b. Chronic anabolic-androgenic steroid treatment during adolescence increases anterior hypothalamic vasopressin and aggression in intact hamsters. *Psychoneuroendocrinology* 25, 317–338.
- Heinrichs, M., Domes, G., 2008. Neuropeptides and social behaviour: effects of oxytocin and vasopressin in humans. *Prog. Brain Res.* 170, 337–350.
- Hjarvard, B.M., Larsen, O.N., Juul-Madsen, H.R., Jorgensen, E., Jensen, K.H., 2009. Social rank influences the distribution of blood leukocyte subsets in female growing pigs. *Scand. J. Lab. Anim. Sci.* 36, 309–320.
- Hofmann, H.A., Benson, M.E., Fernald, R.D., 1999. Social status regulates growth rate: consequences for life-history strategies. *Proc. Natl. Acad. Sci. U.S.A.* 96, 14171–14176.
- Höglund, E., Balm, P.H., Winberg, S., 2000. Skin darkening, a potential social signal in subordinate arctic charr (*Salvelinus alpinus*): the regulatory role of brain monoamines and pro-opiomelanocortin-derived peptides. *J. Exp. Biol.* 203 Pt 11, 1711–1721.
- Höglund, E., Kolm, N., Winberg, S., 2001. Stress-induced changes in brain serotonergic activity, plasma cortisol and aggressive behavior in Arctic charr (*Salvelinus alpinus*) is counteracted by L-DOPA. *Physiol. Behav.* 74, 381–389.
- Höglund, E., Balm, P.H., Winberg, S., 2002. Behavioural and neuroendocrine effects of environmental background colour and social interaction in Arctic charr (*Salvelinus alpinus*). *J. Exp. Biol.* 205, 2535–2543.
- Höglund, E., Korzan, W.J., Watt, M.J., Forster, G.L., Summers, T.R., Johannessen, H.F., Renner, K.J., Summers, C.H., 2005. Effects of L-DOPA on aggressive behavior and central monoaminergic activity in the lizard *Anolis carolinensis*, using a new method for drug delivery. *Behav. Brain Res.* 156, 53–64.
- Holand, O., Gjostein, H., Losvar, A., Kumpula, J., Smith, M.E., Roed, K.H., Nieminen, M., Weladji, R.B., 2004. Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *J. Zool.* 263, 365–372.
- Horner, M., Weiger, W.A., Edwards, D.H., Kravitz, E.A., 1997. Excitation of identified serotonergic neurons by escape command neurons in lobsters. *J. Exp. Biol.* 200 (Pt 14), 2017–2033.
- Hostetter, C.M., Ryabinin, A.E., 2013. The CRF system and social behavior: a review. *Front. Neurosci.* 7, 92.
- Huang, S., Li, G., Pan, Y., Song, M., Zhao, J., Wan, X., Krebs, C.J., Wang, Z., Han, W., Zhang, Z., 2020. Density-induced social stress alters oxytocin and vasopressin activities in the brain of a small rodent species. *Integr. Zool.*
- Huber, R., Panksepp, J.B., Yue, Z., Delago, A., Moore, P., 2001. Dynamic interactions of behavior and amine neurochemistry in acquisition and maintenance of social rank in crayfish. *Brain Behav. Evol.* 57, 271–282.
- Huhman, K.L., Solomon, M.B., Janicki, M., Harmon, A.C., Lin, S.M., Israel, J.E., Jasnow, A.M., 2003. Conditioned defeat in male and female Syrian hamsters. *Horm. Behav.* 44, 293–299.
- Jaeger, R.G., Wang, H.G., Kohn, N.R., Cross, H.S., 2005. Displacement of territorial aggression by male Red-Backed Salamanders. *J. Herpetol.* 39, 653–656.

- Jasnaw, A.M., Huhman, K.L., Bartness, T.J., Demas, G.E., 2002. Short days and exogenous melatonin increase aggression of male Syrian hamsters (*Mesocricetus auratus*). *Horm. Behav.* 42, 13–20.
- Jenssen, T.A., Decourcy, K.R., Congdon, J.D., 2005. Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? *Anim. Behav.* 69, 1325–1336.
- Jiang, B., Wang, F., Yang, S., Fang, P., Deng, Z.F., Xiao, J.L., Hu, Z.L., Chen, J.G., 2014. SKF83959 produces antidepressant effects in a chronic social defeat stress model of depression through BDNF-TrkB pathway. *Int. J. Neuropsychopharmacol.* 18.
- Johansen, I.B., Sorensen, C., Sandvik, G.K., Nilsson, G.E., Hoglund, E., Bakken, M., Øverli, Ø., 2012. Neural plasticity is affected by stress and heritable variation in stress coping style. *Comp. Biochem. Physiol. Genom. Proteomics* 7, 161–171.
- Johnson, E.T., Snyder-Mackler, N., Beehner, J.C., Bergman, T.J., 2014. Kinship and dominance rank influence the strength of social bonds in female geladas (*Theropithecus gelada*). *Int. J. Primatol.* 35, 288–304.
- Jones, S.R., Fernyhough, C., 2007. A new look at the neural diathesis–stress model of schizophrenia: the primacy of social-evaluative and uncontrollable situations. *Schizophr. Bull.* 33, 1171–1177.
- Karavanich, C., Atema, J., 1998. Individual recognition and memory in lobster dominance. *Anim. Behav.* 56, 1553–1560.
- Keeney, A., Jessop, D.S., Harbuz, M.S., Marsden, C.A., Hogg, S., Blackburn-Munro, R.E., 2006. Differential effects of acute and chronic social defeat stress on hypothalamic-pituitary-adrenal axis function and hippocampal serotonin release in mice. *J. Neuroendocrinol.* 18, 330–338.
- Keifer, J., Summers, C.H., 2016. Putting the "biology" back into "neurobiology": the strength of diversity in animal model systems for neuroscience research. *Front. Syst. Neurosci.* 10, 69.
- Kelley, J.L., Rodgers, G.M., Morrell, L.J., 2016. Conflict between background matching and social signalling in a colour-changing freshwater fish. *R Soc Open Sci* 3, 160040.
- Kendrick, K.M., 2006. Introduction. The neurobiology of social recognition, attraction and bonding. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 361, 2057–2059.
- Kim, J., Pignatelli, M., Xu, S., Itoharu, S., Tonegawa, S., 2016. Antagonistic negative and positive neurons of the basolateral amygdala. *Nat. Neurosci.* 19, 1636–1646.
- King, A.J., Cowlishaw, G., 2007. When to use social information: the advantage of large group size in individual decision making. *Biol. Lett.* 3, 137–139.
- Kittilsen, S., Schjolden, J., Beitnes-Johansen, I., Shaw, J.C., Pottinger, T.G., Sorensen, C., Braastad, B.O., Bakken, M., Øverli, Ø., 2009. Melanin-based skin spots reflect stress responsiveness in salmonid fish. *Horm. Behav.* 56, 292–298.
- Kittilsen, S., Johansen, I.B., Braastad, B.O., Øverli, Ø., 2012. Pigments, parasites and personality: towards a unifying role for steroid hormones? *PLoS One* 7, e34281.
- Kiyokawa, Y., Takeuchi, Y., Mori, Y., 2007. Two types of social buffering differentially mitigate conditioned fear responses. *Eur. J. Neurosci.* 26, 3606–3613.
- Klemfuss, H., Southerland, S., Britton, K.T., 1998. Cardiovascular actions of neuropeptide Y and social stress. *Peptides* 19, 85–92.
- Koolhaas, J.M., De Boer, S.F., De Rutter, A.J., Meerlo, P., Sgoifo, A., 1997a. Social stress in rats and mice. *Acta Physiol. Scand. Suppl.* 640, 69–72.
- Koolhaas, J.M., Meerlo, P., De Boer, S.F., Strubbe, J.H., Bohus, B., 1997b. The temporal dynamics of the stress response. *Neurosci. Biobehav. Rev.* 21, 775–782.
- Koolhaas, J.M., Korte, S.M., de Boer, S.F., van der Vegt, B.J., van Reenen, C.G., Hopster, H., de Jong, I.C., Ruijs, M.A., Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress physiology. *Neurosci. Biobehav. Rev.* 23, 925–935.
- Koolhaas, J.M., de Boer, S.F., Buwalda, B., van Reenen, K., 2007. Individual variation in coping with stress: a multidimensional approach of ultimate and proximate mechanisms. *Brain Behav. Evol.* 70, 218–226.
- Koolhaas, J.M., Bartolomucci, A., Buwalda, B., de Boer, S.F., Flugge, G., Korte, S.M., Meerlo, P., Murison, R., Olivier, B., Palanza, P., Richter-Levin, G., Sgoifo, A., Steimer, T., Stiedl, O., van Dijk, G., Wöhr, M., Fuchs, E., 2011. Stress revisited: a critical evaluation of the stress concept. *Neurosci. Biobehav. Rev.* 35, 1291–1301.
- Koot, S., Zoratto, F., Cassano, T., Colangeli, R., Laviola, G., van den Bos, R., Adriani, W., 2012. Compromised decision-making and increased gambling proneness following dietary serotonin depletion in rats. *Neuropharmacology* 62, 1640–1650.
- Koren, L., Mokady, O., Gefen, E., 2006. Elevated testosterone levels and social ranks in female rock hyrax. *Horm. Behav.* 49, 470–477.
- Korte, S.M., Smit, J., Bouws, G.A., Koolhaas, J.M., Bohus, B., 1990. Behavioral and neuroendocrine response to psychosocial stress in male rats: the effects of the 5-HT_{1A} agonist ipsapirone. *Horm. Behav.* 24, 554–567.
- Korzan, W.J., Summers, T.R., Ronan, P.J., Summers, C.H., 2000a. Visible sympathetic activity as a social signal in *Anolis carolinensis*: changes in aggression and plasma catecholamines. *Horm. Behav.* 38, 193–199.
- Korzan, W.J., Summers, T.R., Summers, C.H., 2000b. Monoaminergic activities of limbic regions are elevated during aggression: influence of sympathetic social signaling. *Brain Res.* 870, 170–178.
- Korzan, W.J., Summers, T.R., Summers, C.H., 2002. Manipulation of visual sympathetic sign stimulus modifies social status and plasma catecholamines. *Gen. Comp. Endocrinol.* 128, 153–161.
- Korzan, W.J., Summers, C.H., 2004. Serotonergic response to social stress and artificial social sign stimuli during paired interactions between male *Anolis carolinensis*. *Neuroscience* 123, 835–845.
- Korzan, W.J., Fernald, R.D., 2005. Color of territorial male cichlids predicts agonistic behavior towards conspecifics. *Horm. Behav.* 48, 109.
- Korzan, W.J., Øverli, Ø., Summers, C.H., 2006. Future social rank: forecasting status in the green anole (*Anolis carolinensis*). *Acta Ethol.* 9, 48–57.
- Korzan, W.J., Höglund, E., Watt, M.J., Forster, G.L., Øverli, Ø., Lukkes, J.L., Summers, C.H., 2007. Memory of opponents is more potent than visual sign stimuli after social hierarchy has been established. *Behav. Brain Res.* 183, 31–42.
- Korzan, W.J., Summers, C.H., 2007. Behavioral diversity and neurochemical plasticity: selection of stress coping strategies that define social status. *Brain Behav. Evol.* 70, 257–266.
- Korzan, W.J., Robison, R.R., Zhao, S., Fernald, R.D., 2008. Color change as a potential behavioral strategy. *Horm. Behav.* 54, 463–470.
- Korzan, W.J., Summers, T.R., Summers, C.H., 2021. Neural and endocrine responses to social stress differ during actual and virtual aggressive interactions or physiological sign stimuli. *Behav. Process.* 182, 104294.
- Krishnan, V., Han, M.H., Graham, D.L., Berton, O., Renthal, W., Russo, S.J., Laplant, Q., Graham, A., Lutter, M., Lagace, D.C., Ghose, S., Reister, R., Tannous, P., Green, T.A., Neve, R.L., Chakravarty, S., Kumar, A., Eisch, A.J., Self, D.W., Lee, F.S., Tamminga, C.A., Cooper, D.C., Gershenfeld, H.K., Nestler, E.J., 2007. Molecular adaptations underlying susceptibility and resistance to social defeat in brain reward regions. *Cell* 131, 391–404.
- Kromrey, S., Czoty, P., Rowe, M., Nader, M., 2014. Cognitive performance and homeage activity in female cynomolgus monkeys: relationship to social rank and cocaine reinforcement. *FASEB J.* 28.
- Krugers, H.J., Koolhaas, J.M., Bohus, B., Korf, J., 1993. A single social stress-experience alters glutamate receptor-binding in rat hippocampal CA3 area. *Neurosci. Lett.* 154, 73–77.
- Kruk, M.R., van der Poel, A.M., Vos-Frerichs, T.P., 1979. The induction of aggressive behaviour by electrical stimulation in the hypothalamus of male rats. *Behaviour* 70, 292–322.
- Kruk, M.R., Westphal, K.G., van Erp, A.M., van Asperen, J., Cave, B.J., Slater, E., de Koning, J., Haller, J., 1998. The hypothalamus: cross-roads of endocrine and behavioural regulation in grooming and aggression. *Neurosci. Biobehav. Rev.* 23, 163–177.
- Kumsta, R., Chen, F.S., Pape, H.C., Heinrichs, M., 2013. Neuropeptide S receptor gene is associated with cortisol responses to social stress in humans. *Biol. Psychol.* 93, 304–307.
- Lailvaux, S.P., Herrel, A., Vanhooydonck, B., Meyers, J.J., Irschick, D.J., 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc. Biol. Sci.* 271, 2501–2508.
- Laredo, S.A., Steinman, M.Q., Robles, C.F., Ferrer, E., Ragen, B.J., Trainor, B.C., 2015. Effects of defeat stress on behavioral flexibility in males and females: modulation by the mu-opioid receptor. *Eur. J. Neurosci.* 41, 434–441.
- Larrieu, T., Sandi, C., 2018. Stress-induced depression: is social rank a predictive risk factor? *Bioessays* 40, e1800012.
- Larson, E.T., Summers, C.H., 2001. Serotonin reverses dominant social status. *Behav. Brain Res.* 121, 95–102.
- Larson, E.T., O'Malley, D.M., Melloni Jr., R.H., 2006. Aggression and vasotocin are associated with dominant-subordinate relationships in zebrafish. *Behav. Brain Res.* 167, 94–102.
- Lee, T.J., Zanello, A.F., Morrison, T.R., Ricci, L.A., Melloni Jr., R.H., 2021. Valproate selectively suppresses adolescent anabolic/androgenic steroid-induced aggressive behavior: implications for a role of hypothalamic gamma-aminobutyric acid neural signaling. *Behav. Pharmacol.*
- Lepage, O., Larson, E.T., Mayer, I., Winberg, S., 2005. Serotonin, but not melatonin, plays a role in shaping dominant-subordinate relationships and aggression in rainbow trout. *Horm. Behav.* 48, 233–242.
- Leroy, F., Park, J., Asok, A., Brann, D.H., Meira, T., Boyle, L.M., Buss, E.W., Kandel, E.R., Siegelbaum, S.A., 2018. A circuit from hippocampal CA2 to lateral septum disinhibits social aggression. *Nature* 564, 213–218.
- Lewin, N.S., Treidel, L.M., Place, N.J., Holekamp, K.E., Haussmann, M.F., 2014. Social rank predicts telomere length in female spotted hyenas (*Crocuta crocuta*). *Integr. Comp. Biol.* 54, E122. E122.
- Li, L., Gao, X., Zhou, Q., 2018. Absence of fear renewal and functional connections between prefrontal cortex and hippocampus in infant mice. *Neurobiol. Learn. Mem.* 152, 1–9.
- Lightman, S.L., Windle, R.J., Julian, M.D., Harbuz, M.S., Shanks, N., Wood, S.A., Kershaw, Y.M., Ingram, C.D., 2000. Significance of pulsatility in the HPA axis. *Novartis Found. Symp.* 227, 244–257.
- Lightman, S.L., Windle, R.J., Ma, X.M., Harbuz, M.S., Shanks, N.M., Julian, M.D., Wood, S.A., Kershaw, Y.M., Ingram, C.D., 2002. Hypothalamic-pituitary-adrenal function. *Arch. Physiol. Biochem.* 110, 90–93.
- Lightman, S.L., 2008. The neuroendocrinology of stress: a never ending story. *J. Neuroendocrinol.* 20, 880–884.
- Lin, D., Boyle, M.P., Dollar, P., Lee, H., Lein, E.S., Perona, P., Anderson, D.J., 2011. Functional identification of an aggression locus in the mouse hypothalamus. *Nature* 470, 221–226.
- Lin, Q., Lin, J.D., Huang, L.M., 2009. Effects of substrate color, light intensity and temperature on survival and skin color change of juvenile seahorses, *Hippocampus erectus* Perry, 1810. *Aquaculture* 298, 157–161.
- Ling, T.J., Forster, G.L., Watt, M.J., Korzan, W.J., Renner, K.J., Summers, C.H., 2009. Social status differentiates rapid neuroendocrine responses to restraint stress. *Physiol. Behav.* 96, 218–232.
- Ling, T.J., Summers, C.H., Renner, K.J., Watt, M.J., 2010. Opponent recognition and social status differentiate rapid neuroendocrine responses to social challenge. *Physiol. Behav.* 99, 571–578.
- Lorenzi, V., Carpenter, R.E., Summers, C.H., Earley, R.L., Grober, M.S., 2009. Serotonin, social status and sex change in the bluebanded goby *Lythrypnus dalli*. *Physiol. Behav.* 97, 476–483.
- Lozano-Montes, L., Astori, S., Abad, S., Guillot de Suduiraut, I., Sandi, C., Zalachoras, I., 2019. Latency to reward predicts social dominance in rats: a causal role for the dopaminergic mesolimbic system. *Front. Behav. Neurosci.* 13, 69.

- Lu, A., Borries, C., 2004. Social and spatial costs of dominance rank in female Hanuman langurs. *Am. J. Primatol.* 62, 66–67.
- Lucas, L.R., Celen, Z., Tamashiro, K.L., Blanchard, R.J., Blanchard, D.C., Markham, C., Sakai, R.R., McEwen, B.S., 2004. Repeated exposure to social stress has long-term effects on indirect markers of dopaminergic activity in brain regions associated with motivated behavior. *Neuroscience* 124, 449–457.
- Lukkes, J., Vuong, S., Scholl, J., Oliver, H., Forster, G., 2009. Corticotropin-releasing factor receptor antagonism within the dorsal raphe nucleus reduces social anxiety-like behavior after early-life social isolation. *J. Neurosci.* 29, 9955–9960.
- Luppino, D., Moul, C., Hawes, D.J., Brennan, J., Dadds, M.R., 2014. Association between a polymorphism of the vasopressin 1B receptor gene and aggression in children. *Psychiatr. Genet.* 24, 185–190.
- Maier, S.F., 1990. Role of fear in mediating shuttle escape learning deficit produced by inescapable shock. *J. Exp. Psychol. Anim. Behav. Process.* 16, 137–149.
- Maier, S.F., Watkins, L.R., 2005. Stressor controllability and learned helplessness: the roles of the dorsal raphe nucleus, serotonin, and corticotropin-releasing factor. *Neurosci. Biobehav. Rev.* 29, 829–841.
- Mallei, A., Ieraci, A., Popoli, M., 2019. Chronic social defeat stress differentially regulates the expression of BDNF transcripts and epigenetic modifying enzymes in susceptible and resilient mice. *World J. Biol. Psychiatr.* 20, 555–566.
- Maruska, K.P., Carpenter, R.E., Fernald, R.D., 2012. Characterization of cell proliferation throughout the brain of the African cichlid fish *Astatotilapia burtoni* and its regulation by social status. *J. Comp. Neurol.* 520, 3471–3491.
- Maruska, K.P., Zhang, A., Neboori, A., Fernald, R.D., 2013. Social opportunity causes rapid transcriptional changes in the social behaviour network of the brain in an African cichlid fish. *J. Neuroendocrinol.* 25, 145–157.
- Maruska, K.P., Fernald, R.D., 2018. *Astatotilapia burtoni*: a model system for analyzing the neurobiology of behavior. *ACS Chem. Neurosci.* 9, 1951–1962.
- Maruska, K.P., Sohn, Y.C., Fernald, R.D., 2019. Mechanistic target of rapamycin (mTOR) implicated in plasticity of the reproductive axis during social status transitions. *Gen. Comp. Endocrinol.* 282, 113209.
- Matter, J.M., Ronan, P.J., Summers, C.H., 1998. Central monoamines in free-ranging lizards: differences associated with social roles and territoriality. *Brain Behav. Evol.* 51, 23–32.
- Maxson, S.C., Canastar, A., 2003. Conceptual and methodological issues in the genetics of mouse agonistic behavior. *Horm. Behav.* 44, 258–262.
- McEwen, B.S., 2000. Effects of adverse experiences for brain structure and function. *Biol. Psychiatry* 48, 721–731.
- McIntyre, D.C., Chew, G.L., 1983. Relation between social rank, submissive behavior, and brain catecholamine levels in ring-necked pheasants (*Phasianus colchicus*). *Behav. Neurosci.* 97, 595–601.
- McKittrick, C.R., Blanchard, D.C., Blanchard, R.J., McEwen, B.S., Sakai, R.R., 1995. Serotonin receptor binding in a colony model of chronic social stress. *Biol. Psychiatr.* 37, 383–393.
- McKittrick, C.R., Magarinos, A.M., Blanchard, D.C., Blanchard, R.J., McEwen, B.S., Sakai, R.R., 2000. Chronic social stress reduces dendritic arbors in CA3 of hippocampus and decreases binding to serotonin transporter sites. *Synapse* 36, 85–94.
- McLott, J., Jurecic, J., Hemphill, L., Dunn, K.S., 2013. Development of an amygdalocentric neurocircuitry-reactive aggression theoretical model of emergence delirium in posttraumatic stress disorder: an integrative literature review. *AANA J. (Am. Assoc. Nurse Anesth.)* 81, 379–384.
- Meaney, M.J., Bhatnagar, S., Larocque, S., McCormick, C., Shanks, N., Sharma, S., Smythe, J., Viau, V., Plotsky, P.M., 1993. Individual differences in the hypothalamic-pituitary-adrenal stress response and the hypothalamic CRF system. *Ann. N. Y. Acad. Sci.* 697, 70–85.
- Meerlo, P., Overkamp, G.J., Koolhaas, J.M., 1997. Behavioural and physiological consequences of a single social defeat in Roman high- and low-avoidance rats. *Psychoneuroendocrinology* 22, 155–168.
- Meerlo, P., Sgoifo, A., De Boer, S.F., Koolhaas, J.M., 1999. Long-lasting consequences of a social conflict in rats: behavior during the interaction predicts subsequent changes in daily rhythms of heart rate, temperature, and activity. *Behav. Neurosci.* 113, 1283–1290.
- Melloni Jr., R.H., Ricci, L.A., 2010. Adolescent exposure to anabolic/androgenic steroids and the neurobiology of offensive aggression: a hypothalamic neural model based on findings in pubertal Syrian hamsters. *Horm. Behav.* 58, 177–191.
- Meyer, W.N., Keifer, J., Korzan, W.J., Summers, C.H., 2004. Social stress and corticosterone regionally upregulate limbic N-methyl-D-aspartate receptor (NR) subunit type NR(2A) and NR(2B) in the lizard *Anolis carolinensis*. *Neuroscience* 128, 675–684.
- Miczek, K.A., Weerts, E.M., DeBold, J.F., 1993. Alcohol, benzodiazepine-GABA A receptor complex and aggression: ethological analysis of individual differences in rodents and primates. *J. Stud. Alcohol Suppl.* 11, 170–179.
- Miczek, K.A., Weerts, E.M., Vivian, J.A., Barros, H.M., 1995. Aggression, anxiety and vocalizations in animals: GABA A and 5-HT anxiolytics. *Psychopharmacology (Berlin)* 121, 38–56.
- Miczek, K.A., Hussain, S., Faccidomo, S., 1998. Alcohol-heightened aggression in mice: attenuation by 5-HT 1A receptor agonists. *Psychopharmacology (Berlin)* 139, 160–168.
- Miczek, K.A., Maxson, S.C., Fish, E.W., Faccidomo, S., 2001. Aggressive behavioral phenotypes in mice. *Behav. Brain Res.* 125, 167–181.
- Miczek, K.A., de Almeida, R.M., Kravitz, E.A., Rissman, E.F., de Boer, S.F., Raine, A., 2007. Neurobiology of escalated aggression and violence. *J. Neurosci.* 27, 11803–11806.
- Milzter, K., Reinhard, H.J., 1983. Comparative studies of the social rank positions in female and male-rats. *Zeitschrift Fur Versuchstierkunde* 25, 170, 170.
- Miyai, C.A., Carretero Sanches, F.H., Costa, T.M., Colpo, K.D., Volpato, G.L., Barreto, R. E., 2011. The correlation between subordinate fish eye colour and received attacks: a negative social feedback mechanism for the reduction of aggression during the formation of dominance hierarchies. *Zoology (Jena)* 114, 335–339.
- Moltesen, M., Laursen, D.C., Thornqvist, P.O., Andersson, M.A., Winberg, S., Høglund, E., 2016. Effects of acute and chronic stress on telencephalic neurochemistry and gene expression in rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* 219, 3907–3914.
- Monder, C., Sakai, R.R., Miroff, Y., Blanchard, D.C., Blanchard, R.J., 1994. Reciprocal changes in plasma corticosterone and testosterone in stressed male rats maintained in a visible burrow system: evidence for a mediating role of testicular 11 beta-hydroxysteroid dehydrogenase. *Endocrinology* 134, 1193–1198.
- Moravcová, S., Cervena, K., Mikova, H., Pacesova, D., Pallag, G., Novotny, J., Bendova, Z., 2020. Social defeat stress affects resident's clock gene and bdnf expression in the brain. *Stress* 1–7.
- Morgan, D., Grant, K.A., Prioleau, O.A., Nader, S.H., Kaplan, J.R., Nader, M.A., 2000. Predictors of social status in cynomolgus monkeys (*Macaca fascicularis*) after group formation. *Am. J. Primatol.* 52, 115–131.
- Morris, R.G., Inglis, J., Ainge, J.A., Olverman, H.J., Tulloch, J., Dudai, Y., Kelly, P.A., 2006. Memory reconsolidation: sensitivity of spatial memory to inhibition of protein synthesis in dorsal hippocampus during encoding and retrieval. *Neuron* 50, 479–489.
- Morrison, T.R., Ricci, L.A., Melloni Jr., R.H., 2015. Anabolic/androgenic steroid administration during adolescence and adulthood differentially modulates aggression and anxiety. *Horm. Behav.* 69C, 132–138.
- Morrison, T.R., Ricci, L.A., Puckett, A.S., Joyce, J., Curran, R., Davis, C., Melloni Jr., R. H., 2020. Serotonin type-3 receptors differentially modulate anxiety and aggression during withdrawal from adolescent anabolic steroid exposure. *Horm. Behav.* 119, 104650.
- Mueller, T., 2005. The effects of social rank on growth patterns in captive adolescent female baboons (*Papio hamadryas anubis*). *Am. J. Primatol.* 66, 198–199.
- Mul, J.D., Soto, M., Cahill, M.E., Ryan, R.E., Takahashi, H., So, K., Zheng, J., Croote, D.E., Hirshman, M.F., la Fleur, S.E., Nestler, E.J., Goodyear, L.J., 2018. Voluntary wheel running promotes resilience to chronic social defeat stress in mice: a role for nucleus accumbens DeltaFosB. *Neuropsychopharmacology* 43, 1934–1942.
- Muske, L.E., Fernald, R.D., 1987a. Control of a teleost social signal. II. Anatomical and physiological specializations of chromatophores. *J. Comp. Physiol. [A]* 160, 99–107.
- Muske, L.E., Fernald, R.D., 1987b. Control of a teleost social signal. I. Neural basis for differential expression of a color pattern. *J. Comp. Physiol. [A]* 160, 89–97.
- Nasrallah, P., Haidar, E.A., Stephan, J.S., El Hayek, L., Karnib, N., Khalifeh, M., Barmo, N., Jabre, V., Houbeika, R., Ghanem, A., Nasser, J., Zeeni, N., Bassil, M., Sleiman, S.F., 2019. Branched-chain amino acids mediate resilience to chronic social defeat stress by activating BDNF/TRKB signaling. *Neurobiol. Stress* 11, 100170.
- Nevison, C.M., Rayment, F.D.G., Simpson, M.J.A., 1996. Birth sex ratios and maternal social rank in a captive colony of rhesus monkeys (*Macaca mulatta*). *Am. J. Primatol.* 39, 123–138.
- Nikulina, E.M., Lacagnina, M.J., Fanous, S., Wang, J., Hammer Jr., R.P., 2012. Intermittent social defeat stress enhances mesocorticolimbic DeltaFosB/BDNF co-expression and persistently activates corticotelomeric neurons: implication for vulnerability to psychostimulants. *Neuroscience* 212, 38–48.
- Nocjar, C., Zhang, J., Feng, P., Panksepp, J., 2012. The social defeat animal model of depression shows diminished levels of orexin in mesocortical regions of the dopamine system, and of dynorphin and orexin in the hypothalamus. *Neuroscience* 218, 138–153.
- Nowacka, M.M., Paul-Samojedny, M., Bielecka, A.M., Obuchowicz, E., 2014. Chronic social instability stress enhances vulnerability of BDNF response to LPS in the limbic structures of female rats: a protective role of antidepressants. *Neurosci. Res.* 88, 74–83.
- O'Connor, K.I., Metcalfe, N.B., Taylor, A.C., 1999. Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Anim. Behav.* 58, 1269–1276.
- Orsini, C.A., Maren, S., 2012. Neural and cellular mechanisms of fear and extinction memory formation. *Neurosci. Biobehav. Rev.* 36, 1773–1802.
- Øverli, Ø., Winberg, S., Damsgjrd, B., Jobling, M., 1998. Food intake and spontaneous swimming activity in Arctic char (*Salvelinus alpinus*): role of brain serotonergic activity and social interactions. *Can. J. Zool.* 76, 1366–1370.
- Øverli, Ø., Harris, C.A., Winberg, S., 1999. Short-term effects of fights for social dominance and the establishment of dominant-subordinate relationships on brain monoamines and cortisol in rainbow trout. *Brain Behav. Evol.* 54, 263–275.
- Øverli, Ø., Korzan, W.J., Larson, E.T., Lepage, O., Pottinger, T.G., Winberg, S., Renner, K. J., Summers, C.H., 2002a. Short-term social stress increases aggression in territorial fish. *Nature* (submitted for publication).
- Øverli, Ø., Kotzian, S., Winberg, S., 2002b. Effects of cortisol on aggression and locomotor activity in rainbow trout. *Horm. Behav.* 42, 53–61.
- Øverli, Ø., Korzan, W.J., Høglund, E., Winberg, S., Bollig, H., Watt, M., Forster, G.L., Barton, B.A., E, O.V., Renner, K.J., Summers, C.H., 2004a. Stress coping style predicts aggression and social dominance in rainbow trout. *Horm. Behav.* 45, 235–241.
- Øverli, Ø., Korzan, W.J., Larson, E.T., Winberg, S., Lepage, O., Pottinger, T.G., Renner, K. J., Summers, C.H., 2004b. Behavioral and neuroendocrine correlates of displaced aggression in trout. *Horm. Behav.* 45, 324–329.
- Øverli, Ø., Sorensen, C., Pulman, K.G., Pottinger, T.G., Korzan, W., Summers, C.H., Nilsson, G.E., 2007. Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neurosci. Biobehav. Rev.* 31, 396–412.

- Pang, T., Yaeger, J.D.W., Summers, C.H., Mitra, R., 2021. Cardinal role of the environment in stress induced changes across life stages and generations. *Neurosci. Biobehav. Rev.* 124, 137–150.
- Panksepp, J., Burgdorf, J., Beinfeld, M.C., Kroes, R.A., Moskal, J.R., 2007. Brain regional neuropeptide changes resulting from social defeat. *Behav. Neurosci.* 121, 1364–1371.
- Parikh, V.N., Clement, T., Fernald, R.D., 2006. Physiological consequences of social descent: studies in *Astatotilapia burtoni*. *J. Endocrinol.* 190, 183–190.
- Park, M.J., Seo, B.A., Lee, B., Shin, H.S., Kang, M.G., 2018. Stress-induced changes in social dominance are scaled by AMPA-type glutamate receptor phosphorylation in the medial prefrontal cortex. *Sci. Rep.* 8, 15008.
- Parr, L.A., Winslow, J.T., Hopkins, W.D., de Waal, F.B., 2000. Recognizing facial cues: individual discrimination by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *J. Comp. Psychol.* 114, 47–60.
- Pearson, B.L., Crawley, J.N., Eilam, D., Pentkowski, N.S., Summers, C.H., 2017. Curiosity as an approach to ethoexperimental analysis: behavioral neuroscience as seen by students and colleagues of Bob Blanchard. *Neurosci. Biobehav. Rev.* 76, 415–422.
- Pelletier, F., Festa-Bianchet, M., 2006. Sexual selection and social rank in bighorn rams. *Anim. Behav.* 71, 649–655.
- Petty, F., Kramer, G., Wilson, L., Chae, Y.L., 1993. Learned helplessness and in vivo hippocampal norepinephrine release. *Pharmacol., Biochem. Behav.* 46, 231–235.
- Petty, F., Chae, Y., Kramer, G., Jordan, S., Wilson, L., 1994a. Learned helplessness sensitizes hippocampal norepinephrine to mild stress. *Biol. Psychiatr.* 35, 903–908.
- Petty, F., Kramer, G., Wilson, L., Jordan, S., 1994b. In vivo serotonin release and learned helplessness. *Psychiatr. Res.* 52, 285–293.
- Petty, F., Kramer, G.L., Wu, J., 1997. Serotonergic modulation of learned helplessness. *Ann. N. Y. Acad. Sci.* 821, 538–541.
- Pi, G., Gao, D., Wu, D., Wang, Y., Lei, H., Zeng, W., Gao, Y., Yu, H., Xiong, R., Jiang, T., Li, S., Wang, X., Guo, J., Zhang, S., Yin, T., He, T., Ke, D., Li, R., Li, H., Liu, G., Yang, X., Luo, M.H., Zhang, X., Yang, Y., Wang, J.Z., 2020. Posterior basolateral amygdala to ventral hippocampal CA1 drives approach behaviour to exert an anxiolytic effect. *Nat. Commun.* 11, 183.
- Potegal, M., Huhman, K., Moore, T., Meyerhoff, J., 1993. Conditioned defeat in the Syrian golden hamster (*Mesocricetus auratus*). *Behav. Neural Biol.* 60, 93–102.
- Potts, J.R., Lewis, M.A., 2016. How memory of direct animal interactions can lead to territorial pattern formation. *J. R. Soc. Interface* 13.
- Price, S.M., Luong, K., Bell, R.S., Rose, G.J., 2018. Latency for facultative expression of male-typical courtship behaviour by female bluehead wrasses depends on social rank: the 'priming/gating' hypothesis. *J. Exp. Biol.* 221.
- Ramsay, S.M., Ratcliffe, L.M., 2003. Determinants of social rank in female black-capped chickadees (*Poecile atricapilla*). *Can. J. Zool.* 81, 117–121.
- Razzoli, M., Domenici, E., Carboni, L., Rantamaki, T., Lindholm, J., Castren, E., Arban, R., 2011. A role for BDNF/TrkB signaling in behavioral and physiological consequences of social defeat stress. *Gene Brain Behav.* 10, 424–433.
- Renevey, N., Bshary, R., van de Waal, E., 2013. Philopatric vervet monkey females are the focus of social attention rather independently of rank. *Behaviour* 150, 599–615.
- Ricci, L., Summers, C.H., Larson, E.T., O'Malley, D., Melloni, R.H., 2013. Development of aggressive phenotypes in zebrafish: interactions of age, experience and social status. *Anim. Behav.* 86, 245–252.
- Ricci, L.A., Grimes, J.M., Melloni Jr., R.H., 2004. Serotonin type 3 receptors modulate the aggression-stimulating effects of adolescent cocaine exposure in Syrian hamsters (*Mesocricetus auratus*). *Behav. Neurosci.* 118, 1097–1110.
- Ricci, L.A., Knyshevski, I., Melloni Jr., R.H., 2005. Serotonin type 3 receptors stimulate offensive aggression in Syrian hamsters. *Behav. Brain Res.* 156, 19–29.
- Ricci, L.A., Connor, D.F., Morrison, R., Melloni Jr., R.H., 2007. Risperidone exerts potent anti-aggressive effects in a developmentally immature animal model of escalated aggression. *Biol. Psychiatr.* 62, 218–225.
- Riedel, J., Polansky, L., Wittig, R.M., Boesch, C., 2020. Social rank overrides environmental and community fluctuations in determining meat access by female chimpanzees in the Tai National Park, Cote d'Ivoire. *PeerJ* 8.
- Robertson, J.M., Prince, M.A., Achua, J.K., Carpenter, R.E., Arendt, D.H., Smith, J.P., Summers, T.L., Summers, T.R., Summers, C.H., 2015. Nuance and behavioral cogency: how the visible burrow system inspired the stress-alternatives model and conceptualization of the continuum of anxiety. *Physiol. Behav.* 146, 86–97.
- Robertson, J.M., Achua, J.K., Smith, J.P., Prince, M.A., Staton, C.D., Ronan, P.J., Summers, T.R., Summers, C.H., 2017. Anxious behavior induces elevated hippocampal Cb2 receptor gene expression. *Neuroscience* 352, 273–284.
- Ross, A.P., McCann, K.E., Larkin, T.E., Song, Z., Grieb, Z.A., Huhman, K.L., Albers, H.E., 2019. Sex-dependent effects of social isolation on the regulation of arginine-vasopressin (AVP) V1a, oxytocin (OT) and serotonin (5HT) 1a receptor binding and aggression. *Horm. Behav.* 116, 104578.
- Rozeske, R.R., Evans, A.K., Frank, M.G., Watkins, L.R., Lowry, C.A., Maier, S.F., 2011. Uncontrollable, but not controllable, stress desensitizes 5-HT1A receptors in the dorsal raphe nucleus. *J. Neurosci.* 31, 14107–14115.
- Rubenstein, D.L., 1978. On predation, competition, and the advantages of group living. In: (Ed.), *Social Behavior. Vol. Perspectives in Ethology Volume 3*. Springer Nature, pp. 205–231.
- Ruis, M.A., te Brake, J.H., Buwalda, B., De Boer, S.F., Meerlo, P., Korte, S.M., Blokhuis, H. J., Koolhaas, J.M., 1999. Housing familiar male wildtype rats together reduces the long-term adverse behavioural and physiological effects of social defeat. *Psychoneuroendocrinology* 24, 285–300.
- Ruiz-Gomez Mde, L., Kittilsen, S., Høglund, E., Huntingford, F.A., Sorensen, C., Pottinger, T.G., Bakken, M., Winberg, S., Korzan, W.J., Øverli, Ø., 2008. Behavioral plasticity in rainbow trout (*Oncorhynchus mykiss*) with divergent coping styles: when doves become hawks. *Horm. Behav.* 54, 534–538.
- Ruiz-Gomez Mde, L., Huntingford, F.A., Øverli, Ø., Thornqvist, P.O., Høglund, E., 2011. Response to environmental change in rainbow trout selected for divergent stress coping styles. *Physiol. Behav.* 102, 317–322.
- Sajdyk, T.J., Johnson, P.L., Leitermann, R.J., Fitz, S.D., Dietrich, A., Morin, M., Gehlert, D.R., Urban, J.H., Shekhar, A., 2008. Neuropeptide Y in the amygdala induces long-term resilience to stress-induced reductions in social responses but not hypothalamic-adrenal-pituitary axis activity or hyperthermia. *J. Neurosci.* 28, 893–903.
- Sandi, C., Woodson, J.C., Haynes, V.F., Park, C.R., Touyarot, K., Lopez-Fernandez, M.A., Venero, C., Diamond, D.M., 2005. Acute stress-induced impairment of spatial memory is associated with decreased expression of neural cell adhesion molecule in the hippocampus and prefrontal cortex. *Biol. Psychiatry* 57, 856–864.
- Santamaria-Garcia, H., Burgaleta, M., Sebastian-Galles, N., 2015. Neuroanatomical markers of social hierarchy recognition in humans: a combined ERP/MRI study. *J. Neurosci.* 35, 10843–10850.
- Sapolsky, R.M., 1982. The endocrine stress-response and social status in the wild baboon. *Horm. Behav.* 16, 279–292.
- Sapolsky, R.M., 1983. Individual differences in cortisol secretory patterns in the wild baboon: role of negative feedback sensitivity. *Endocrinology* 113, 2263–2267.
- Sapolsky, R.M., 1985. Stress-induced suppression of testicular function in the wild baboon: role of glucocorticoids. *Endocrinology* 116, 2273–2278.
- Sapolsky, R.M., 1987. Stress, social status, and reproductive physiology in free-living baboons. In: Crews, D. (Ed.), *Psychobiology of Reproductive Behavior an Evolutionary Perspective*. Prentice-Hall, Inc., Englewood Cliffs, NJ, pp. 292–322.
- Sapolsky, R.M., 1988. Individual differences and the stress response: studies of a wild primate. *Adv. Exp. Med. Biol.* 245, 399–411.
- Sapolsky, R.M., 1989. Hypercortisolism among socially subordinate wild baboons originates at the CNS level. *Arch. Gen. Psychiatry* 46, 1047–1051.
- Sapolsky, R.M., 1990. A. E. Bennett Award paper. Adrenocortical function, social rank, and personality among wild baboons. *Biol. Psychiatr.* 28, 862–878.
- Sapolsky, R.M., 1991. Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology* 16, 281–293.
- Sapolsky, R.M., 1992. Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology* 17, 701–709.
- Schjolden, J., Basic, D., Winberg, S., 2009. Aggression in rainbow trout is inhibited by both MR and GR antagonists. *Physiol. Behav.* 98, 625–630.
- Schuurman, T., 1980. Hormonal correlates of agonistic behavior in adult male rats. *Prog. Brain Res.* 53, 415–420.
- Schwartz, J.J., Morrison, R.L., Ricci, L.A., Melloni Jr., R.H., 2009. Paliperidone suppresses the development of the aggressive phenotype in a developmentally sensitive animal model of escalated aggression. *Psychopharmacology (Berlin)* 203, 653–663.
- Schwartz, J.J., Melloni Jr., R.H., 2010a. Dopamine activity in the lateral anterior hypothalamus modulates AAS-induced aggression through D2 but not D5 receptors. *Behav. Neurosci.* 124, 645–655.
- Schwartz, J.J., Melloni Jr., R.H., 2010b. Anterior hypothalamic dopamine D2 receptors modulate adolescent anabolic/androgenic steroid-induced offensive aggression in the Syrian hamster. *Behav. Pharmacol.* 21, 314–322.
- Schwartz, J.J., Ricci, L.A., Melloni Jr., R.H., 2013. Prior fighting experience increases aggression in Syrian hamsters: implications for a role of dopamine in the winner effect. *Aggress. Behav.* 39, 290–300.
- Selye, H., 1984. *The Stress of Life*. McGraw-Hill Book Co., New York.
- Selye, H., 1985. The nature of stress. *Basal Facts* 7, 3–11.
- Sensar, K., Kandel, F.L., Godwin, J., 2001. Manipulations of the AVT system shift social status and related courtship and aggressive behavior in the bluehead wrasse. *Horm. Behav.* 40, 21–31.
- Sgoifo, A., de Boer, S.F., Haller, J., Koolhaas, J.M., 1996. Individual differences in plasma catecholamine and corticosterone stress responses of wild-type rats: relationship with aggression. *Physiol. Behav.* 60, 1403–1407.
- Sgoifo, A., Koolhaas, J., De Boer, S., Musso, E., Stilli, D., Buwalda, B., Meerlo, P., 1999. Social stress, autonomic neural activation, and cardiac activity in rats. *Neurosci. Biobehav. Rev.* 23, 915–923.
- Shalev, I., Israel, S., Uzevovsky, F., Gritsenko, I., Kaitz, M., Ebstein, R.P., 2011. Vasopressin needs an audience: neuropeptide elicited stress responses are contingent upon perceived social evaluative threats. *Horm. Behav.* 60, 121–127.
- Shimamoto, A., Debold, J.F., Holly, E.N., Miczek, K.A., 2011. Blunted accumbal dopamine response to cocaine following chronic social stress in female rats: exploring a link between depression and drug abuse. *Psychopharmacology (Berlin)* 218, 271–279.
- Sloman, L., Gilbert, P., Hasey, G., 2002. Evolved mechanisms in depression: the role and interaction of attachment and social rank in depression. *J. Affect. Disord.* (in press).
- Smith, J.P., Achua, J.K., Summers, T.R., Ronan, P.J., Summers, C.H., 2014. Neuropeptide S and BDNF gene expression in the amygdala are influenced by social decision-making under stress. *Front. Behav. Neurosci.* 8, 1–13.
- Smith, J.P., Prince, M.A., Achua, J.K., Robertson, J.M., Anderson, R.T., Ronan, P.J., Summers, C.H., 2016. Intensity of anxiety is modified via complex integrative stress circuitries. *Psychoneuroendocrinology* 63, 351–361.
- Staton, C.D., Yaeger, J.D.W., Khalid, D., Haroun, F., Fernandez, B.S., Fernandez, J.S., Summers, B.K., Summers, T.R., Sathyanesan, M., Newton, S.S., Summers, C.H., 2018. Orexin 2 receptor stimulation enhances resilience, while orexin 2 inhibition promotes susceptibility, to social stress, anxiety and depression. *Neuropharmacology* 143, 79–94.
- Summers, C.H., Norman, M.F., 1988. Chronic low humidity-stress in the lizard *Anolis carolinensis*: changes in diurnal corticosterone rhythms. *J. Exp. Zool.* 247, 271–278.
- Summers, C.H., Greenberg, N., 1994. Somatic correlates of adrenergic activity during aggression in the lizard, *Anolis carolinensis*. *Horm. Behav.* 28, 29–40.

- Summers, C.H., 1995. Regulation of ovarian recrudescence: different effects of corticotropin in small and large female lizards. *Anolis carolinensis* Journal of Experimental Zoology 271, 228–234.
- Summers, C.H., Greenberg, N., 1995. Activation of central biogenic amines following aggressive interaction in male lizards, *Anolis carolinensis*. *Brain Behav. Evol.* 45, 339–349.
- Summers, C.H., Suedkamp, D.A., Grant, T.L., 1995. Regulation of ovarian recrudescence: effects of social-interaction and size on female lizards. *Anolis carolinensis* Journal of Experimental Zoology 271, 235–241.
- Summers, C.H., Larson, E.T., Summers, T.R., Renner, K.J., Greenberg, N., 1998. Regional and temporal separation of serotonergic activity mediating social stress. *Neuroscience* 87, 489–496.
- Summers, C.H., 2001. Mechanisms for quick and variable responses. *Brain Behav. Evol.* 57, 283–292.
- Summers, C.H., 2002. Social interaction over time, implications for stress responsiveness. *Integr. Comp. Biol.* 42, 591–599.
- Summers, C.H., Summers, T.R., Moore, M.C., Korzan, W.J., Woodley, S.K., Ronan, P.J., Hoglund, E., Watt, M.J., Greenberg, N., 2003. Temporal patterns of limbic monoamine and plasma corticosterone response during social stress. *Neuroscience* 116, 553–563.
- Summers, C.H., Forster, G.L., Korzan, W.J., Watt, M.J., Larson, E.T., Øverli, Ø., Hoglund, E., Ronan, P.J., Summers, T.R., Renner, K.J., Greenberg, N., 2005a. Dynamics and mechanics of social rank reversal. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 191, 241–252.
- Summers, C.H., Korzan, W.J., Lukkes, J.L., Watt, M.J., Forster, G.L., Øverli, Ø., Hoglund, E., Larson, E.T., Ronan, P.J., Matter, J.M., Summers, T.R., Renner, K.J., Greenberg, N., 2005b. Does serotonin influence aggression? comparing regional activity before and during social interaction. *Physiol. Biochem. Zool.* 78, 679–694.
- Summers, C.H., Watt, M.J., Ling, T.J., Forster, G.L., Carpenter, R.E., Korzan, W.J., Lukkes, J.L., Øverli, Ø., 2005c. Glucocorticoid interaction with aggression in non-mammalian vertebrates: reciprocal action. *Eur. J. Pharmacol.* 526, 21–35.
- Summers, C.H., Winberg, S., 2006. Interactions between the neural regulation of stress and aggression. *J. Exp. Biol.* 209, 4581–4589.
- Summers, C.H., Yaeger, J.D.W., Staton, C.D., Arendt, D.H., Summers, T.R., 2020. Orexin/hypocretin receptor modulation of anxiolytic and antidepressive responses during social stress and decision-making: potential for therapy. *Brain Res.* 1731, 146085.
- Summers, T.R., Hunter, A.L., Summers, C.H., 1997. Female social reproductive roles affect central monoamines. *Brain Res.* 767, 272–278.
- Summers, T.R., Summers, T.L., Carpenter, R.E., Smith, J.P., Young, S.L., Meyerink, B., Orr, T.Z., Arendt, D.H., Summers, C.H., 2017. Learning and CRF-induced indecision during escape and submission in rainbow trout during socially aggressive interactions in the stress-alternatives model. *Front. Neurosci.* 11, 515.
- Svensson, P.A., Wong, B.B.M., 2011. Carotenoid-based signals in behavioural ecology: a review. *Behaviour* 148, 131–189.
- Takahashi, A., Quadros, I.M., de Almeida, R.M., Miczek, K.A., 2012. Behavioral and pharmacogenetics of aggressive behavior. *Curr Top Behav Neurosci.*
- Takahashi, L.K., Blanchard, R.J., 1982. Attack and defense in laboratory and wild Norway and black rats. *Behav. Process.* 7, 49–62.
- Tamashiro, K.L., Nguyen, M.M., Sakai, R.R., 2005. Social stress: from rodents to primates. *Front. Neuroendocrinol.* 26, 27–40.
- Tanaka, K., Furuhashiki, T., Kitaoka, S., Senzai, Y., Imoto, Y., Segi-Nishida, E., Deguchi, Y., Breyer, R.M., Breyer, M.D., Narumiya, S., 2012. Prostaglandin E₂-mediated attenuation of mesocortical dopaminergic pathway is critical for susceptibility to repeated social defeat stress in mice. *J. Neurosci.* 32, 4319–4329.
- Taylor, S.L., Stanek, L.M., Ressler, K.J., Huhman, K.L., 2011. Differential brain-derived neurotrophic factor expression in limbic brain regions following social defeat of territorial aggression. *Behav. Neurosci.* 125, 911–920.
- Thompson, R.R., George, K., Walton, J.C., Orr, S.P., Benson, J., 2006. Sex-specific influences of vasopressin on human social communication. *Proc. Natl. Acad. Sci. U. S. A.* 103, 7889–7894.
- Thor, D.H., Wainwright, K.L., Holloway, W.R., 1982. Persistence of attention to a novel conspecific: some developmental variables in laboratory rats. *Dev. Psychobiol.* 15, 1–8.
- Tibbetts, E.A., Dale, J., 2007. Individual recognition: it is good to be different. *Trends Ecol. Evol.* 22, 529–537.
- Tidey, J.W., Miczek, K.A., 1996. Social defeat stress selectively alters mesocorticolimbic dopamine release: an in vivo microdialysis study. *Brain Res.* 721, 140–149.
- Tovote, P., Fadok, J.P., Luthi, A., 2015. Neuronal circuits for fear and anxiety. *Nat. Rev. Neurosci.* 16, 317–331.
- Tsukahara, T., Kawase, T., Yoshida, H., Bukawa, W., Kan, T., Toyoda, A., 2019. Preliminary investigation of the effect of oral supplementation of *Lactobacillus plantarum* strain SNK12 on mRNA levels of neurotrophic factors and GABA receptors in the hippocampus of mice under stress-free and sub-chronic mild social defeat-stressing conditions. *Biosci. Biotechnol. Biochem.* 83, 2345–2354.
- Valentino, R.J., Reyes, B., Van Bockstaele, E., Bangasser, D., 2012. Molecular and cellular sex differences at the intersection of stress and arousal. *Neuropharmacology* 62, 13–20.
- Van Kampen, M., Kramer, M., Hiemke, C., Flugge, G., Fuchs, E., 2002. The chronic psychosocial stress paradigm in male tree shrews: evaluation of a novel animal model for depressive disorders. *Stress* 5, 37–46.
- Vaz-Serrano, J., Ruiz-Gomez, M.L., Gjoen, H.M., Skov, P.V., Huntingford, F.A., Øverli, Ø., Hoglund, E., 2011. Consistent boldness behaviour in early emerging fry of domesticated Atlantic salmon (*Salmo salar*): decoupling of behavioural and physiological traits of the proactive stress coping style. *Physiol. Behav.* 103, 359–364.
- Veenema, A.H., Koolhaas, J.M., de Kloet, E.R., 2004. Basal and stress-induced differences in HPA axis, 5-HT responsiveness, and hippocampal cell proliferation in two mouse lines. *Ann. N. Y. Acad. Sci.* 1018, 255–265.
- Veiga, C.P., Miczek, K.A., Lucion, A.B., Almeida, R.M., 2007. Effect of 5-HT_{1B} receptor agonists injected into the prefrontal cortex on maternal aggression in rats. *Braz. J. Med. Biol. Res.* 40, 825–830.
- Vining, C., Iyer, V., Bhatnagar, S., 2007. Intracerebroventricular administration of corticotrophin-releasing hormone receptor antagonists produces different effects on hypothalamic pituitary adrenal responses to novel restraint depending on the stress history of the animal. *J. Neuroendocrinol.* 19, 198–207.
- Vollmayr, B., Faust, H., Lewicka, S., Henn, F.A., 2001. Brain-derived-neurotrophic-factor (BDNF) stress response in rats bred for learned helplessness. *Mol. Psychiatr.* 6, 471–474, 358.
- Volpato, G.L., Luchiarri, A.C., Duarte, C.R.A., Barreto, R.E., Ramanzini, G.C., 2003. Eye color as an indicator of social rank in the fish Nile tilapia. *Braz. J. Med. Biol. Res.* 36, 1659–1663.
- Wall, P.M., Blanchard, R.J., Markham, C., Yang, M., Blanchard, D.C., 2004a. Infralimbic D1 receptor agonist effects on spontaneous novelty exploration and anxiety-like defensive responding in CD-1 mice. *Behav. Brain Res.* 152, 67–79.
- Wall, P.M., Blanchard, R.J., Yang, M., Blanchard, D.C., 2004b. Differential effects of infralimbic vs. ventromedial orbital PFC lidocaine infusions in CD-1 mice on defensive responding in the mouse defense test battery and rat exposure test. *Brain Res.* 1020, 73–85.
- Wang, J., Fanous, S., Terwilliger, E.F., Bass, C.E., Hammer Jr., R.P., Nikulina, E.M., 2013. BDNF overexpression in the ventral tegmental area prolongs social defeat stress-induced cross-sensitization to amphetamine and increases DeltaFosB expression in mesocorticolimbic regions of rats. *Neuropsychopharmacology* 38, 2286–2296.
- Watt, M.J., Forster, G.L., Feng, N., Renner, K.J., Summers, C.H., 2004. Behavioral state influences temporal patterns of limbic monoamine activity during social stress. *Soc. Neurosci. Abs.* 30, 426–429.
- Watt, M.J., Forster, G.L., Korzan, W.J., Renner, K.J., Summers, C.H., 2007. Rapid neuroendocrine responses evoked at the onset of social challenge. *Physiol. Behav.* 90, 567–575.
- Weintraub, A., Singaravelu, J., Bhatnagar, S., 2010. Enduring and sex-specific effects of adolescent social isolation in rats on adult stress reactivity. *Brain Res.* 1343, 83–92.
- Wiley, R.H., 2013. Specificity and multiplicity in the recognition of individuals: implications for the evolution of social behaviour. *Biol. Rev. Camb. Phil. Soc.* 88, 179–195.
- Winberg, S., Nilsson, G.E., Ols, K.H., 1991. Social rank and brain levels of monoamines and monoamine metabolites in Arctic charr, *Salvelinus alpinus* (L.). *J. Comp. Physiol.: Neuroethology, Sensory, Neural, and Behavioral Physiology* 168, 241–246.
- Winberg, S., Nilsson, G.E., 1992. Induction of social dominance by L-dopa treatment in Arctic charr. *Neuroreport* 3, 243–246.
- Winberg, S., Nilsson, G.E., Olsen, K.H., 1992. Changes in brain serotonergic activity during hierarchic behavior in Arctic charr (*Salvelinus alpinus* L.) are socially induced. *J. Comp Physiol [A]*. 170, 93–99.
- Winberg, S., Carter, C.G., McCarthy, I.D., He, Z.Y., Nilsson, G.E., Houlihan, D.F., 1993. Feeding rank and brain serotonergic activity in rainbow trout *Oncorhynchus mykiss*. *J. Exp. Biol.* 179, 197–211.
- Winberg, S., Nilsson, G.E., 1993. Time course of changes in brain serotonergic activity and brain tryptophan levels in dominant and subordinate juvenile arctic charr. *J. Exp. Biol.* 179, 181–195.
- Winberg, S., Winberg, Y., Fernald, R.D., 1997. Effect of social rank on brain monoaminergic activity in a cichlid fish. *Brain Behav. Evol.* 49, 230–236.
- Winberg, S., Lepage, O., 1998. Elevation of brain 5-HT activity, POMC expression, and plasma cortisol in socially subordinate rainbow trout. *Am. J. Physiol.* 274, R645–R654.
- Winberg, S., Øverli, Ø., Lepage, O., 2001. Suppression of aggression in rainbow trout (*Oncorhynchus mykiss*) by dietary L-tryptophan. *J. Exp. Biol.* 204, 3867–3876.
- Wittemyer, G., Polansky, L., Douglas-Hamilton, I., Getz, W.M., 2008. Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. *Proc. Natl. Acad. Sci. U. S. A.* 105, 19108–19113.
- Wood, S.K., Walker, H.E., Valentino, R.J., Bhatnagar, S., 2010. Individual differences in reactivity to social stress predict susceptibility and resilience to a depressive phenotype: role of corticotropin-releasing factor. *Endocrinology* 151, 1795–1805.
- Wood, S.K., Zhang, X.Y., Reyes, B.A., Lee, C.S., Van Bockstaele, E.J., Valentino, R.J., 2013. Cellular adaptations of dorsal raphe serotonin neurons associated with the development of active coping in response to social stress. *Biol. Psychiatr.* 73, 1087–1094.
- Wright, E., Galbany, J., McFarlin, S.C., Ndayishimiye, E., Stoinski, T.S., Robbins, M.M., 2019. Male body size, dominance rank and strategic use of aggression in a group-living mammal. *Anim. Behav.* 151, 87–102.
- Wynn, J.G., 2004. Influence of plio-pleistocene aridification on human evolution! Evidence from paleosols of the turkana basin, Kenya. *Am. J. Phys. Anthropol.* 123, 106–118.
- Xu, H., Wang, J., Jing, H., Ellenbroek, B., Shao, F., Wang, W., 2020. mPFC GABAergic transmission mediated the role of BDNF signaling in cognitive impairment but not anxiety induced by adolescent social stress. *Neuropharmacology* 108412.
- Yaeger, J.D.W., Krupp, K.T., Gale, J.J., Summers, C.H., 2020. Counterbalanced microcircuits for Orx₁ and Orx₂ regulation of stress reactivity. *Medicine in Drug Discovery* 100059, 1–20.
- Yang, E.J., Phelps, S.M., Crews, D., Wilczynski, W., 2001. The effects of social experience on aggressive behavior in *Anolis carolinensis* Ethology, 107, 777–793.

- Yang, E.J., Wilczynski, W., 2002. Relationships between hormones and aggressive behavior in green anole lizards: an analysis using structural equation modeling. *Horm. Behav.* 42, 195–205.
- Yang, E.J., Wilczynski, W., 2003. Interaction effects of corticosterone and experience on aggressive behavior in the green anole lizard. *Horm. Behav.* 44, 281–292.
- Yang, M., Farrokhi, C., Vasconcellos, A., Blanchard, R.J., Blanchard, D.C., 2006. Central infusion of ovine CRF (oCRF) potentiates defensive behaviors in CD-1 mice in the Mouse Defense Test Battery (MDTB). *Behav. Brain Res.* 171, 1–8.
- Yang, Y., Wang, Z.H., Jin, S., Gao, D., Liu, N., Chen, S.P., Zhang, S., Liu, Q., Liu, E., Wang, X., Liang, X., Wei, P., Li, X., Li, Y., Yue, C., Li, H.L., Wang, Y.L., Wang, Q., Ke, D., Xie, Q., Xu, F., Wang, L., Wang, J.Z., 2016. Opposite monosynaptic scaling of BLP-vCA1 inputs governs hopefulness- and helplessness-modulated spatial learning and memory. *Nat. Commun.* 7, 11935.
- Yang, Y., Wang, J.Z., 2017. From structure to behavior in basolateral amygdala-Hippocampus circuits. *Front. Neural Circ.* 11, 86.
- Young, L.J., 2002. The neurobiology of social recognition, approach, and avoidance. *Biol. Psychiatr.* 51, 18–26.
- Zehr, J.L., Van Meter, P.E., Wallen, K., 2005. Factors regulating the timing of puberty onset in female Rhesus monkeys (*Macaca mulatta*): role of prenatal androgens, social rank, and adolescent body weight. *Biol. Reprod.* 72, 1087–1094.
- Zoicas, I., Menon, R., Neumann, I.D., 2016. Neuropeptide S reduces fear and avoidance of con-specifics induced by social fear conditioning and social defeat, respectively. *Neuropharmacology* 108, 284–291.
- Zou, W.J., Song, Y.L., Wu, M.Y., Chen, X.T., You, Q.L., Yang, Q., Luo, Z.Y., Huang, L., Kong, Y., Feng, J., Fang, D.X., Li, X.W., Yang, J.M., Mei, L., Gao, T.M., 2020. A discrete serotonergic circuit regulates vulnerability to social stress. *Nat. Commun.* 11, 4218.