

REVIEW

Modification of feeding circuits in the evolution of social behavior

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ABSTRACT

Adaptive trade-offs between foraging and social behavior intuitively explain many aspects of individual decision-making. Given the intimate connection between social behavior and feeding/foraging at the behavioral level, we propose that social behaviors are linked to foraging on a mechanistic level, and that modifications of feeding circuits are crucial in the evolution of complex social behaviors. In this Review, we first highlight the overlap between mechanisms underlying foraging and parental care and then expand this argument to consider the manipulation of feeding-related pathways in the evolution of other complex social behaviors. We include examples from diverse taxa to highlight that the independent evolution of complex social behaviors is a variation on the theme of feeding circuit modification.

KEY WORDS: Foraging, Feeding behavior, Parental behavior, Social behavior, Evolution, Neural circuits

Introduction

A fundamental question at the intersection of evolution and behavior is how novel behaviors evolve. From an adaptationist perspective, all behavior must maximize trade-offs between current and future reproduction. In the case of social behavior, this means organisms must strike a balance between increasing their energy reserves and expending these reserves on interactions with partners, offspring or group members. Energetics-focused arguments can be applied across time scales (e.g. evolutionary and developmental) and levels of biological organization (Mathot and Dingemanse, 2015; Rittschof et al., 2015). It is noteworthy that amidst all these considerations, social behavior is often intimately linked to feeding/foraging at a basic behavioral level: mate acquisition involves directly or indirectly demonstrating a superior ability to acquire food, parental care involves often extreme forms of offspring provisioning, and many interactions in advanced social systems (e.g. primates, eusocial insects) increase the fitness of related individuals via food provisioning of the family group. Trade-offs between foraging and socializing intuitively explain many aspects of individual decision-making, yet the link between feeding/foraging, social behavior, and their underlying neural and molecular mechanisms has rarely been considered in the context of behavioral evolution (but see Ament et al., 2010; Schneider et al., 2013).

The neural and molecular mechanisms underlying foraging (i.e. food searching) behavior have been identified and are evolutionarily conserved across diverse animal taxa (Konturek et al., 2004; Yapici et al., 2014). These mechanisms integrate internal and external cues to signal energetic need and thereby drive appropriate behavioral

responses. In an immediate sense, these pathways may influence social behavior, for example, by signaling to an animal when to care for, abandon or even eat its offspring to recover valuable energetic resources. Yet how these same mechanisms were initially modified during the evolution of provisioning/feeding behaviors that are important in many social interactions is not understood. Parental behavior is thought to be an evolutionary precursor to more general forms of social behavior (Clutton-Brock, 1991; Linksvayer and Wade, 2005; Royle et al., 2012; Tallamy and Wood, 1986), and indeed, modifications that facilitate provisioning of offspring may well have been co-opted to extend food provisioning behaviors to more distantly related group members. For feeding/provisioning behavior to arise, foraging behavior must be modified such that individuals forage for food, but do not consume it (entirely) themselves. Moreover, in the case of parental care, feeding circuits may also need to be modified to prevent cannibalism of nutrient-rich eggs and/or offspring, and to accommodate the increased energetic demands of offspring care. Thus, the same mechanisms that influence feeding decisions within species are likely to be targets for the evolution of diverse social behaviors among species.

In this Review, we discuss evidence for overlap in the neural and molecular mechanisms mediating feeding/foraging behavior and social behavior across taxa. We propose that the overlap of neural and molecular pathways and related behaviors suggests that modification of feeding mechanisms has repeatedly led to the evolution of parental care and sociality, and independent emergence of these behaviors across vertebrate and invertebrate taxa represent variations on this theme. At present, disparate types of data exist in different systems and we advocate that comparative, integrative and mechanistic studies are needed to further elucidate these questions.

At the intersection of foraging and social behavior

In the most basic context, nutritional ecology can explain much of the group formation or sociality that we see in even the simplest of life forms (Lihoreau et al., 2015). In many ecologically relevant contexts, the abundance of food resources in the environment can drive the self-assembly of individuals into groups (Raubenheimer et al., 2012). A simple example can be found in cellular slime molds (*Dictyostelium discoideum*), where nutrient availability determines whether the cells forage independently or aggregate into a slug-like mass that moves as a multi-cellular fruiting body to produce spores (Gregor et al., 2010). Nutritional state can also contribute to individual decision-making within groups in vertebrates, such as in the three-spined stickleback fish (*Gasterosteus aculeatus*), where hunger levels can change decisions on shoal formation and composition (Frommen et al., 2007). Although these group decision-making examples are interesting, much more is known about how nutritional state alters the behavior of an individual outside of a group context.

In many organisms, the molecules and principal brain regions that govern eating behavior have been described in great detail, especially in the context of eating disorders and obesity. Within this clinical framework, quite a lot is known about orexigenic

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(appetite stimulant) and anorectic (appetite suppressant) hormones that link nutritional state and behavior. As the hormones and brain regions that regulate feeding behavior have been discussed in great depth elsewhere (Murphy and Bloom, 2006; Schwartz et al., 2000; Stanley et al., 2005), we give only a brief overview of the neural and molecular mechanisms regulating feeding behaviour, beginning with signaling molecules in the gut and ending with neuropeptides in the brain. Where data are available, we highlight similarities and differences between vertebrates and invertebrates.

Peptide hormones and feeding behavior

The brain and gut have an intimate connection, as energy homeostasis must be maintained so that animals can take advantage of adaptive behavioral opportunities such as reproduction, as well as overcome environmental challenges such as predation and resource competition (O'Connell and Hofmann, 2011b; Schneider et al., 2013). The periphery communicates nutritional state to the brain through a host of peptide hormones, including (but not limited to) leptin from adipose tissue, ghrelin from the stomach and insulin from the pancreas (Fig. 1A) (Schneider et al., 2013). These peripheral signaling molecules have receptors in brain regions that regulate the production of peptide hormones that modify feeding behavior. Research in laboratory rodents has highlighted many neuropeptides produced in the brain that alter feeding behavior (summarized in Table 1) (Schneider et al., 2013), and invertebrates have homologs to some of these neuropeptides (Audsley and Weaver, 2009; Campbell et al., 2004; Lovejoy and de Lannoy, 2013; Melcher et al., 2007; Nässel and Wegener, 2011). A particularly prominent example is neuropeptide Y (NPY; NPY in insects), which alters feeding behavior in worms (De Bono and Bargmann, 1998), insects (Wu et al., 2003) and all major vertebrate lineages (fish: Lopez-Patino et al., 1999; frogs: Crespi et al., 2004; reptiles: Morris and Crews, 1990; birds: Strader and Buntin, 2001; and mammals: Stanley and Leibowitz, 1984), suggesting an evolutionarily ancient role for this peptide in foraging behavior. Although this remarkable evolutionary

conservation of feeding-related molecules is quite well documented, the involvement of these molecules in the evolution of social behavior is just beginning to be appreciated (Ament et al., 2010; O'Rourke and Renn, 2015; Schneider et al., 2013).

Neural mechanisms of feeding behavior

Although feeding-related molecules and brain regions are well understood in vertebrates, and widespread molecular conservation facilitates comparisons and predictions across taxa, little is known about the neural circuitry underlying feeding behavior in invertebrates (i.e. which brain regions and neurons are involved). Even in vertebrates, highly detailed work probing the neural circuits underlying feeding behavior is largely restricted to rodents. In vertebrates, peripheral signals of nutritional state (leptin, insulin, ghrelin, etc.) are received in the hypothalamus (Fig. 1B). In mammals, the arcuate nucleus of the hypothalamus is the epicenter of integration, where receptors for leptin, insulin, and ghrelin integrate information from the periphery (Barsh and Schwartz, 2002). The arcuate nucleus also contains key regulators of feeding behavior, including NPY, agouti-related protein (AgRP) and galanin neurons (which are generally appetite stimulating) as well as neurons containing cocaine- and amphetamine-related transcript (CART) and α -melanocyte stimulating hormone (α -MSH) (which are generally appetite suppressing) (Schwartz and Porte, 2005). These neuropeptide cells then project to various brain regions, including other subregions of the hypothalamus (periventricular, ventromedial and lateral). Receptors for NPY, AgRP, galanin and α -MSH are widely distributed throughout the rodent brain, suggesting far-reaching influences of nutritional state on brain function. For example, the brain regions mediating feeding also interface with dopaminergic- and opiate-motivational circuitries [such as the ventral tegmental area (VTA)] to influence foraging motivation and learning (Abizaid, 2009). Although the neural basis of feeding/foraging is best understood in laboratory rodents, parallel studies in other vertebrate clades highlight both conserved and diverged roles

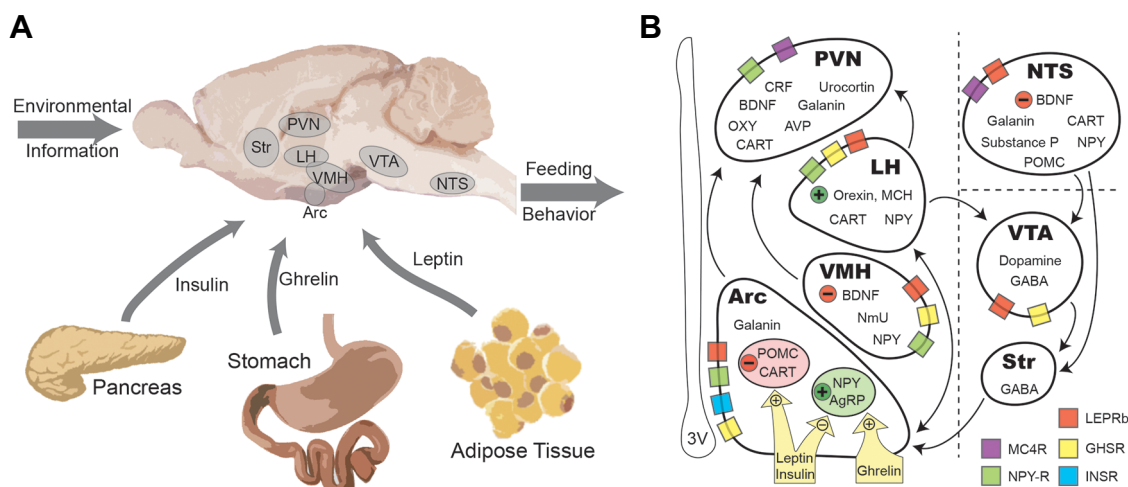


Fig. 1. Integration of environmental and physiological information for adjusting adaptive behavioral output. (A) Peripheral hormones (insulin, ghrelin and leptin, among others) send information to the brain, which integrates environmental information into adaptive feeding behavior via a neural network of brain regions sensitive to peripheral hormones and other feeding-related peptides. Brain regions involved in the classical neural network for feeding are the arcuate nucleus (Arc) near the third ventricle (3V), lateral hypothalamus (LH), nucleus of the solitary tract (NTS), periventricular nucleus of the hypothalamus (PVN), striatum (Str), ventral tegmental area (VTA) and the ventromedial hypothalamus (VMH). (B) Many neuropeptides and their associated receptors modulate feeding behavior, including agouti-related peptide (AgRP), arginine vasopressin (AVP), brain-derived neurotrophic factor (BDNF), cocaine- and amphetamine-regulated transcript (CART), corticotropin-releasing factor (CRF), ghrelin receptor (GHSR), insulin receptor (INSR), long isoform leptin receptor (LEPRb), melanin-concentrating hormone (MCH), neuromedin U (NmU), oxytocin (OXY), melanocortin receptor 4 (MC4R), neuropeptide Y (NPY), neuropeptide Y receptors (NPY-R) and pro-opiomelanocortin (POMC). Receptor distribution is indicated by colored boxes. Plus or minus signs indicate the signaling molecule's effect on appetite, where a plus sign stimulates feeding behavior. Modified from Yeo and Heisler (2012).

Table 1. Peptide hormones important for feeding behavior

Vertebrate peptide	Invertebrate homolog	Effect on feeding behavior	Reference
Agouti-related protein (AgRP)	n/a	Stimulant	Rossi et al., 1998
α -Melanocyte stimulating hormone (α -MSH)	n/a	Suppressant	Murphy et al., 1998
Brain-derived neurotrophic factor (BDNF)	Neurotrophins	Suppressant	Kernie et al., 2000
Cocaine and amphetamine-related transcript (CART)	n/a	Suppressant	Kristensen et al., 1998
Corticotropin releasing factor (CRF)	Diuretic peptides	Suppressant	De Pedro et al., 1993
Galanin	n/a	Stimulant	Corwin et al., 1993
Ghrelin	n/a	Stimulant	Wren et al., 2000
Gonadotropin inhibiting hormone (GnIH)	n/a	Stimulant	Tachibana et al., 2005
Insulin	<i>Drosophila</i> insulin-like proteins (DILPs)	Stimulant	Panksepp and Nance, 1972
Leptin	n/a	Suppressant	Hommel et al., 2006
Neuromedin U	Hugin	Suppressant	Hanada et al., 2004
Neuropeptide Y (NPY)	Neuropeptide F (NPF)	Stimulant	Stanley et al., 1986
Orexin	n/a	Stimulant	Sakurai et al., 1998
Oxytocin	Inatocin	Suppressant	Arletti et al., 1989
Pro-opiomelanocortin (POMC)	n/a	Suppressant	Millington, 2007
Urocortin	n/a	Suppressant	Ohata et al., 2000
n/a	Allatostatins	Suppressant	Hergarden et al., 2012
n/a	Sulfakinins	Suppressant	Wei et al., 2000

for these hypothalamic neuropeptides in the regulation of feeding behavior (Boswell, 2005; Lin et al., 2000). Indeed, the neural distribution of feeding-related peptides overlaps with many brain regions that are hypothesized to influence social behavior across vertebrates (Fig. 2) (O'Connell and Hofmann, 2011a). Notwithstanding that some overlap is surely related to foraging and social behavior being two different classes of goal-directed behavior, the ubiquitous expression of feeding-related peptides in brain regions known to regulate social behavior suggests that these neuropeptides can influence social decision-making. Indeed, it has been proposed that goal-directed behavior initially evolved from neural mechanisms mediating foraging (Hills, 2006).

As feeding behavior is a necessary action in all animals, it is no surprise that invertebrates share some mechanisms that control feeding behavior with vertebrates. Aside from the invertebrate NPF (homolog of the vertebrate NPY) mentioned above, other neuropeptides also regulate invertebrate feeding behavior, including *hugin*, which is homologous to the vertebrate Neuromedin U (Melcher et al., 2007). In *Drosophila*, *hugin* is involved in the decision-making process of whether to eat a novel food source (Melcher and Pankratz, 2005), while in rodents, Neuromedin U suppresses food intake (Howard et al., 2000). There are also some invertebrate-specific neuropeptides that regulate feeding behavior, including allatostatins (Hergarden et al., 2012) and sulfakinins (Wei et al., 2000), which both suppress feeding behavior in insects. Finally, a recent study in *Drosophila* suggests some neurons in the ellipsoid body of the brain central complex stimulate feeding behavior, and are thus functionally similar to the vertebrate AgRP/NPY neurons (Park et al., 2016). However, more work is needed to understand how these neurons function within a larger circuit to promote feeding behavior (Schoofs and Pankratz, 2016).

Overlap in the neural and molecular mechanisms mediating foraging, social behavior and motivation may facilitate social decision-making. Although most laboratory animals are given food *ad libitum*, food resources can drastically fluctuate in the wild, leading animals to display a broader range of behaviors based on nutrient availability. It is not surprising that molecules regulating feeding are also implicated in social behavior changes given that alternative foraging strategies may be adaptive in the changing nutrient landscape, and both foraging and social behaviors fall more

generally into the category of goal-directed behavior. Perhaps what is more interesting is how these evolutionarily ancient molecules and pathways are modified to facilitate more complex social behaviors, such as parental care and sociality.

Coordination of feeding and parenting circuits

The link between social behavior and foraging/feeding behaviors is particularly evident in the provisioning and protection of offspring. For species that exhibit parental care, which has evolved independently in almost every major animal lineage, care of offspring is a major energetic cost of reproduction. Parental care is typically studied in the context of brain regions and molecules that govern social behavior (e.g. oxytocin) (Bales et al., 2004) and stress [e.g. corticotropin releasing factor (CRF), cortisol] (Bales et al., 2006; Lee et al., 2006), which have been extensively reviewed elsewhere (Dulac et al., 2014; Meaney, 2001; Rilling and Young, 2014). However, evidence is accumulating that feeding behavior and parental care are also tightly linked at a mechanistic level (O'Rourke and Renn, 2015). The relationship between feeding regulation and parental behavior varies with life history strategy and ecology. In some situations, feeding behavior and parental care may be antagonistic, such that food consumption needs to be inhibited in order for parental behavior to occur. This may happen to repress infanticide, to inhibit parental feeding behavior in species that exhibit food provisioning to offspring, or in the special case of mouthbrooding animals where eating does not occur during offspring incubation. In contrast, parental care in some species is linked to hyperphagia (increased food intake) to meet the energetic demands of providing food and care to offspring. We discuss evidence that neural mechanisms that regulate feeding and care of offspring are intertwined across independent origins and distinct strategies of parental care (Fig. 3). We group care strategies based on whether they should increase or decrease parental feeding and foraging behaviors and provide specific examples in support of these broad classifications.

Feeding-related peptides in rodent parental care

The onset of parental care is facilitated by a symphony of hormones that orchestrate a switch from apathy or aggression towards offspring to intense and elaborate care behaviors (Numan, 2007; Rilling and Young, 2014). Behavioral outcomes of non-parental

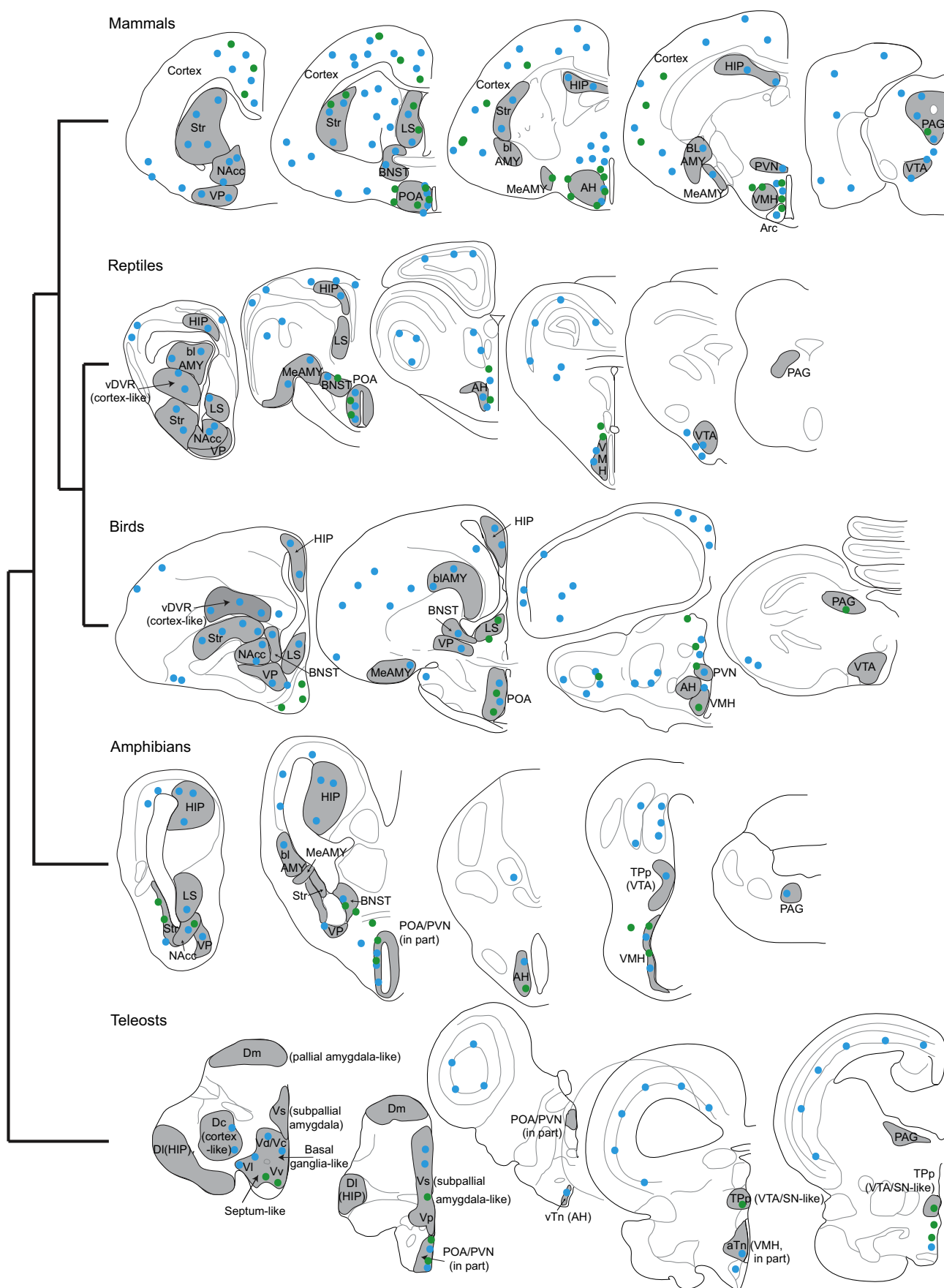


Fig. 2. See next page for legend.

Fig. 2. Overlap of social and feeding-related pathways are conserved in the vertebrate brain. Regions involved in social decision-making across vertebrates are shaded gray and greatly overlap with neuroanatomical locations of NPY neurons (blue) and galanin neurons (green) [other peptides important for feeding behavior including agouti-related peptide (AgRP), urocortins, α -MSH (α -melanocyte stimulating hormone) and CART (cocaine- and amphetamine-regulated transcript) are not known for many vertebrate lineages and thus are not shown]. Figure adapted from O'Connell and Hofmann (2012) with adjustments suggested in Goodson and Kingsbury (2013) and Karten (2013). AH, anterior hypothalamus; bAMY, basolateral amygdala; BNST/MeAMY, bed nucleus of the stria terminalis/medial amygdala; HIP, hippocampus; LS, lateral septum; NAcc, nucleus accumbens; PAG/CG, periaqueductal gray/central gray; POA, preoptic area; Str, striatum; VMH, ventromedial hypothalamus; VP, ventral pallidum; VTA, ventral tegmental area. Distribution for NPY and galanin are from the following publications: mammals – Chronwall et al. (1985), De Quidt and Emson (1986) and Skofitsch and Jacobowitz (1985); reptiles – Bennis et al. (2001), Jiménez et al. (1994) and Medina et al. (1992); birds – Azumaya and Tsutsui (1996), Esposito et al. (2001), Józsa and Mess (1993) and Singh et al. (2013); amphibians – Danger et al. (1985), Lázár et al. (1991), Oliverreau and Oliverreau (1992) and Perroteau et al. (1988); and teleost fish – Anglade et al. (1994) and Cerdá-Reverter et al. (2000).

animals towards conspecific young have been most extensively studied in rodents, where infanticide and caretaking are influenced by genotype, sex and experience (Jakubowski and Terkel, 1985; Lonstein and De Vries, 2000). These studies have found that both male and female wild mice will kill conspecific pups whereas laboratory mice tend to display some level of parental behavior (Jakubowski and Terkel, 1982). Interestingly, male laboratory mice display a time-dependent change in infanticide behavior, where infanticide is inhibited between 12 and 50 days after mating (Vom Saal, 1985), roughly the time frame pups would be present. This

inhibition of infanticidal behavior is facilitated by galanin neurons in the preoptic area of the hypothalamus (Wu et al., 2014). Indeed, optogenetic stimulation of preoptic galanin neurons was sufficient to switch the behavior of laboratory male mice from infanticide to active parental behavior (Wu et al., 2014). It is important to note here that infanticide entails not only the killing of pups, but the eating of pups by the attacker as well. In rodents, galanin and the galanin-like peptide (encoded by separate genes) are colocalized in the hypothalamus and interact with galanin receptors (with varying affinities) to produce seemingly opposite behavioral effects. Galanin stimulates food consumption in satiated rats (Crawley, 1999), where rats are more selective about their food choices (Adams et al., 2008). Galanin also inhibits sexual behavior in males (Poggioli et al., 1992). In contrast, the galanin-like peptide decreases feeding behavior and increases sexual behavior (Fraleigh et al., 2004; Gottsch et al., 2004). This body of work in rodents suggests that galanin and galanin-like peptide neurons regulate not only feeding behavior but reproductive and parental behavior as well. Clearly, more studies are needed to determine the neural circuitry underlying the ability of these neurons to regulate paternal care, sexual behavior and feeding. Moreover, a crucial piece of missing information is the identity of the causal signaling molecule being produced in these neurons that inhibits infanticide and induces parental care. The crosstalk between parental and feeding circuits is supported by additional evidence from urocortin peptides that bind the CRF receptors, and are best known for their role in stress and appetite (Spina et al., 1996). Interestingly, urocortin II both suppresses feeding behavior in rats (Ohata and Shibasaki, 2004) and induces spontaneous parental behavior in male and female prairie voles (*Microtus ochrogaster*) (Samuel et al., 2008). It is clearly crucial to inhibit the eating of offspring by parents, and the link between feeding-related peptides and suppression of infanticide behavior in parental rodents warrants future research.

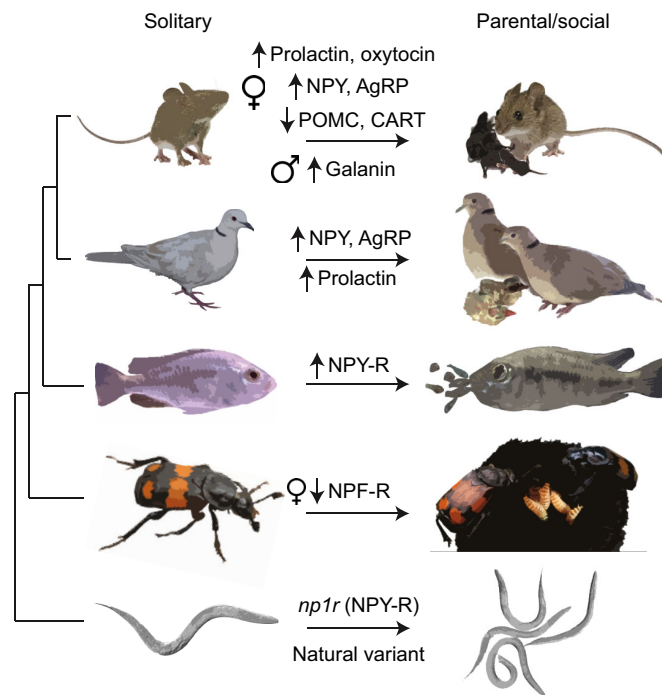


Fig. 3. Summary of how feeding-related pathways are modified as animals transition from solitary to parental/social. Sex-specific effects are noted with male and female symbols. AgRP, agouti-related peptide; NPY, neuropeptide Y; NPF-R, neuropeptide F receptor; NPY-R, neuropeptide Y receptor; POMC, pro-opiomelanocortin [includes α -MSH (melanocyte-stimulating hormone)]. See 'Coordination of feeding and parenting circuits' for references.

Parental care and decreased feeding behavior

In some modes of parental care, parents must reallocate food resources to their offspring rather than themselves. This is especially prominent in species where offspring are altricial, meaning they depend on parents for nourishment. The most obvious example of this behavior is in birds, where many species provide some form of parental care to altricial offspring (Cockburn, 2006). Surprisingly little is known about the neurobiology of avian parental care in the context of foraging and food provisioning to offspring in the nest. However, the regulation of feeding-related peptides and their associated receptors at the onset of parental behavior also occurs in invertebrates. The burying beetle (*Nicrophorus vespilloides*) displays a fascinating array of biparental behavior tightly linked to foraging (Scott, 1998). After securing a carcass for mating, the male and female will maintain the carcass to retard microbial growth and feed their begging offspring pre-digested carrion. As parents must feed their offspring (rather than themselves) and resist eating their own offspring, feeding circuits are likely to be targeted in the evolution of parental care in this system. Indeed, similar to male mice, female burying beetles exhibit a time-dependent inhibition of infanticide following carcass acquisition and mating (Oldekop et al., 2007). Moreover, gene expression of the NPF receptor, but not the NPF peptide, decreases in both males and females during active caring, suggesting the NPY pathway modifies feeding motivation/behavior during active parental care (Cunningham et al., 2016). Interestingly, these same NPF pathways have also been utilized in the evolution of complex insect societies (discussed in detail below).

In some special cases of parental care, species incubate offspring in a way that impedes food intake. Some frogs exhibit this type of parental behavior, including incubation of tadpoles in the vocal sac of male Darwin's frog (*Rhinoderma darwinii*), where offspring receive nutrients from male secretions in addition to absorbing nutrients from the yolk (Goicoechea et al., 1986). Another fascinating example of unique incubation styles in anurans is the now extinct gastric-brooding frog (*Rheobatrachus*; Corben et al., 1974), in which offspring were incubated in the mother's stomach (Tyler et al., 1983). The best-studied examples of the adaptive behavioral trade-offs between feeding and mouthbrooding are in fish, where in some species, females or males protect their fry by housing them in the mouth cavity for several weeks. Remarkably, parents do not eat during this period of mouthbrooding, and this form of parental care has evolved many times in cichlid fish (Goodwin et al., 1998). Interestingly, filial cannibalism has also been described in many species of mouthbrooding fish. Both field and laboratory studies suggest that filial cannibalism occurs because of an energetic trade-off when parental food deprivation becomes too great and offspring are consumed as an alternative food source (Manica, 2002). In the mouthbrooding cichlid *Astatotilapia burtoni*, brain gene expression of neuropeptides that regulate reproduction and feeding are altered during the mouthbrooding period in females (Grone et al., 2012). Moreover, expression of an NPY receptor is higher in mouthbrooding females compared with food-deprived females, suggesting a role of the NPY pathway in mouthbrooding behavior. It is currently unknown how mouthbrooding alters neural mechanisms associated with feeding behavior, although this would certainly lend insight into how parental behavior and feeding interact.

When there is a clear conflict between parental and offspring nutrition, such as provisioning young in beetles or mouthbrooding in cichlids, there is an adaptive trade-off between current (offspring nutrition) and future (parental nutrition) reproductive potential. More comparative and ecologically relevant studies are needed to determine the neural and molecular mechanisms mediating interactions between feeding and parenting and how widespread these interactions are across independent evolutionary transitions to parental behavior.

Offspring provisioning and increased feeding behavior

In contrast to systems in which food intake is inhibited during parental care, there are many examples of parental care strategies that require increased food intake (hyperphagia) to meet the energetic demands of provisioning young. Some vertebrate species provision offspring with food that is manufactured by the parents themselves (rather than foraging for food items to give to their young). This physiological food production requires increased efforts in foraging to meet increased energetic demands. Perhaps the best understood non-mammalian example is in ring doves (*Streptopelia risoria*), where both males and females produce a 'crop milk' that is regurgitated and fed to begging offspring (Lehrman, 1955). Ring dove parents increase their foraging activity during this time of parental care, which is correlated with increased plasma prolactin levels (Goldsmith et al., 1981) and expression of NPY and AgRP in the hypothalamus compared with non-breeding doves (Ramakrishnan et al., 2007; Strader and Buntin, 2003). Interestingly, both food deprivation and prolactin treatment increase hypothalamic NPY and AgRP expression in non-breeding doves, suggesting foraging behavior is increased in response to physiological changes associated with parental behavior in this species. NPY treatment also increases feeding behavior in ring

doves, consistent with the hypothesis that prolactin-induced hyperphagia is in part NPY dependent (Strader and Buntin, 2001). The effect of prolactin on mediating parental behavior in ring doves seems to be brain region specific even within the hypothalamus, as lesions of the preoptic area inhibit many parental behaviors, including the feeding of crop milk to young, but do not affect prolactin-induced hyperphagia (Slawski and Buntin, 1995). There are still many remaining questions on how parental behavior is facilitated in ring doves and a fruitful line of investigation would be examining the relationship between brain regions important for feeding behavior and neural circuits typically related to social behavior in other contexts.

The most energetically demanding effort of parenting in mammals is lactation, during which females increase their food intake and alter energy expenditure and storage (Smith and Grove, 2002; Woodside et al., 2012). The relationship between feeding-related circuitry and that of parental behavior is well understood thanks to extensive studies in laboratory rodents (Crowley, 2015). In brief, expression of hypothalamic NPY and AgRP are increased in lactating rats while expression of pro-opiomelanocortin (POMC) and CART is decreased (Chen et al., 1999; Malabu et al., 1994; Smith, 1993). AgRP in particular is important for increased food intake during lactation, as ablations of AgRP neurons prevent hyperphagia in lactating rats without altering milk production or nursing behavior (Phillips and Palmiter, 2008). Similarly, knockdown of the NPY Y5 receptor in the hypothalamus decreases food intake and maternal nesting behavior in lactating rats (Ladyman and Woodside, 2009). Furthermore, the increase in hypothalamic NPY and AgRP expression and decrease in circulating leptin are dependent on the suckling stimulus of pups (Brogan et al., 1999; Li et al., 1998). Given that suckling behavior induces release of prolactin and oxytocin in the maternal brain (Grosvenor et al., 1986), this suggests a potential modulatory role of prolactin and oxytocin on expression of feeding-related peptides. Our knowledge of the neural correlates of lactation in rodents is making great strides, but many questions remain, such as how hyperphagia is mediated in the brain in a way that prevents eating offspring, if the peptides involved in lactation alter other maternal behaviors; how facilitation of feeding and maternal care occurs at the neural circuit level; and how these findings translate to non-rodent mammals.

The involvement of peptide hormones and hypothalamic brain regions in offspring provisioning and hyperphagia in other species that provision offspring from their own energy reserves remains to be determined. For example, some amphibians, including South American and Malagasy poison frogs, provision offspring with trophic eggs for many weeks until tadpoles complete metamorphosis (Heying, 2001; Weygoldt, 1987). This costly effort of feeding tadpoles trophic eggs correlates with a higher investment across fewer offspring compared with other amphibians. Presumably, this behavior of feeding tadpoles trophic eggs relies on increased foraging efforts for maternal females, although this remains to be investigated. Clearly, more comparative work is needed to understand the sophisticated interplay of peptide hormones in coordinating feeding behavior, parental provisioning and the evolution of novel provisioning strategies.

To eat or not to eat: research at the intersection of feeding and parental behavior

Given that parental care is often an energetically demanding task, it is not surprising that feeding-related molecules and brain regions overlap and may modulate the neural circuitry underlying parental

behavior (Fig. 2). There are many paths forward that would shed light on how the evolution of parental behavior involves changes in feeding mechanisms. Given that parental care has evolved multiple times independently, a comparative approach utilizing diverse species with diverse care strategies will help to identify general principles in underlying neural and molecular mechanisms (Fig. 3). In particular, work on the neural circuits involved in feeding behavior in invertebrates is severely lacking, while broad-scale surveys of gene expression are uncommon in vertebrates but prevalent in insects (see details below). More specific questions include how sensory pathways involved in recognition of offspring and food interface with feeding circuits to drive adaptive behavioral output at the individual level. Furthermore, while laboratory rodents are useful for addressing detailed mechanistic questions, more ecologically relevant experiments will determine how genotype, environment, other ecological factors (such as prey availability) and offspring survivorship impinge on behavioral plasticity and adaptive trade-offs between parenting and foraging.

Modification of foraging circuits in the evolution of sociality

We discuss above how the modification of feeding circuits may be important in the evolution of parental care. Parental care behaviors are, in turn, thought to be an evolutionary antecedent to sociality (Clutton-Brock, 1991; Royle et al., 2012). Eusociality is often cited as social behavior at its most extreme, as most individuals within eusocial societies forgo reproduction entirely to facilitate the reproductive success of one or a few closely related individuals. Non-reproductive individuals generally perform brood care, food-provisioning to the colony and colony defense (Nowak et al., 2010). The most well-studied examples of eusocial behaviors come from hymenopterans (ants, bees, wasps), and specifically the honey bee, *Apis mellifera*. Though little is known about the brain regions involved in feeding behavior in invertebrates, elegant work in honey bees and related species has demonstrated links between the molecular mechanisms of maternal care, the molecular mechanisms of feeding/foraging behaviors, and the maintenance and evolution of sociality within and among species.

Honey bee colonies consist of a single, reproductive queen and many non-reproductive workers. Workers begin as ‘nurses’, performing brood care within the hive. At approximately 2–3 weeks of age workers begin to leave the hive in search of pollen and nectar, spending the rest of their 5–7 week life as ‘foragers’ (Seeley, 2009). While nursing and foraging represent distinct behavioral states, both center around food provisioning: in the case of nurses, brood care (i.e. feeding) within the hive, and in the case of foragers, foraging for food to provision the colony. Given the intimate link between feeding and social behavior in honey bees, it is no surprise that evolutionary and behavioral links between varying degrees of feeding and foraging behavior, parental behavior and sociality have been proposed and substantiated in this and related species (Ament et al., 2010; Linksvayer and Wade, 2005; Tallamy and Wood, 1986).

Overlap of feeding mechanisms involved in maternal care and sociality

The idea that sibling care evolved from maternal care was proposed particularly early on for hymenopterans (Evans and Eberhard, 1970; Hunt, 1999; Wheeler, 2015). Evidence that worker care behavior did indeed evolve from maternal care comes from the primitively eusocial wasp (*Polistes metricus*). In primitively eusocial species, the distinction between worker and reproductive castes is less well defined than in highly eusocial species, and both workers and

reproductives exhibit provisioning behavior across the lifetime of a colony. Thus, *Polistes* affords the opportunity to compare brain gene expression signatures associated with brood care in both reproductive and non-reproductive castes. Gene expression in *Polistes* workers is more similar to that of caring reproductives than non-caring reproductives, suggesting similar gene expression patterns associated with care behavior in mothers and non-parental care givers (Toth et al., 2007). Moreover, many of these differentially expressed genes are implicated in the regulation of brood care and foraging in honey bees (see next section).

Additional evidence for selection on mechanisms important in maternal care in the evolution of eusociality comes from studies of the yolk-storage protein *vitellogenin* (*Vg*). In honey bees, increased levels of circulating *Vg* are associated with increased foraging for pollen, and by extension, increased provisioning of the colony (Page and Amdam, 2007; Page et al., 2006). Within colonies, nurses have higher *Vg* expression and more ovarioles than foragers, indicating that nurse bees performing brood care exhibit a reproductive physiology more similar to that of mothers despite being non-reproductive themselves (Amdam et al., 2006). In addition, *Vg* and its interaction with juvenile hormone and insulin signaling regulate maternal effects on caste determination in ants (Libbrecht et al., 2013), and changes in *Vg* are associated with behavioral transitions to parental care in both male and female burying beetles (Parker et al., 2015; Roy-Zokan et al., 2015). In concert, these studies present evidence that mechanisms mediating maternal care have been selected upon during the evolution of sociality.

Modification of feeding circuits in the evolution of eusociality

In addition to evidence for evolutionary transitions to sociality via maternal care, studies in insects provide evidence for a direct evolutionary link between feeding/foraging behaviors and eusociality. At a broad scale, shared gene expression signatures characterize three independent transitions to eusociality in bees (Woodard et al., 2011). While there is evidence for selection on both shared and distinct gene sets associated with the evolutionary transition from solitary to primitively eusocial and highly eusocial lifestyles, many of the genes under selection in both eusocial groups fall into the same broad classes of biological processes (e.g. carbohydrate metabolism; Woodard et al., 2011). Similarly, within honey bees, brain gene expression profiles predict behavioral differences between nurse and forager bees, and sets of differentially expressed genes are enriched for foraging and energy metabolism pathways (Whitfield et al., 2003). Thus, broad-scale surveys of gene expression within and across species suggest repeated targeting of feeding- and foraging-related pathways in the evolution of insect societies.

Beyond broad-scale gene expression surveys, a number of specific foraging-related genes have been linked to behavioral maturation from nursing to foraging in bees. The *foraging* (*for*) gene was first characterized in *Drosophila*, in which naturally occurring allelic variants give rise to distinct larval foraging strategies (Osborne et al., 1997). This gene also mediates behavioral maturation in honey bees and, as its name implies, is elevated when individuals transition from nursing to foraging (Ben-Shahar et al., 2003). Similarly, increases in the gene *malvolio* (*mvl*), a manganese transporter initially described in *Drosophila* mutants with taste deficiencies (Rodrigues et al., 1995), and NPY are also associated with behavioral maturation to foraging in honey bees (Ben-Shahar et al., 2004). Interestingly, homologs of the NPY pathway also mediate transitions from solitary to social (grouping) behavior in *Caenorhabditis elegans* (De Bono and Bargmann, 1998) and

Drosophila larvae (Wu et al., 2003), suggesting that the role of NPY/NPF in the mediation of social behaviors may be particularly ancient and well conserved across animals. Finally, honey bee foragers have increased insulin production and sensitivity (Ament et al., 2008) despite having lower lipid stores (Toth et al., 2005; Toth and Robinson, 2005). It is crucial to note that manipulations of these genes involved in feeding behavior also cause changes in the timing of behavioral maturation in honey bees, demonstrating that differences in foraging-related pathways are indeed causal in inducing a behavioral shift central to the maintenance of eusocial societies (reviewed in Ament et al., 2010). In sum, both broad-scale patterns of gene expression and detailed studies of individual genes support an important mechanistic link between foraging and sociality. As with maternal behaviors, these studies present evidence for selection on mechanisms mediating feeding and foraging in the evolution of social behavior across hymenopterans and the developmental regulation and maintenance of these behaviors within honey bees.

Variations on the theme of foraging and social behavior

Given that modifications in mechanisms underlying feeding and parental care appear to be key players in the evolution of eusociality, what can these patterns reveal about how transitions to social behavior are evolved and maintained? First, while there is evidence that some changes occur via sequence evolution (Woodard et al., 2011), many behavioral differences are related to changes in the timing and level of gene expression. This observation underlines predictions and empirical evidence that changes in the expression of conserved genes are central to the evolution of social behavior (Linksvayer and Wade, 2005; Robinson and Ben-Shahar, 2002). Furthermore, studies in honey bees reveal not only gene regulatory changes, but also adjustments in response thresholds that are responsible for the evolution of diverse behaviors from shared molecular substrates (e.g. Ben-Shahar, 2005). In other words, existing molecular pathways are modified to change the ‘set point’ of underlying networks in a manner that influences animal behavior and decision-making. Importantly, changes in expression combined with changes in sensitivity help explain behavioral differences at both evolutionary and developmental time scales. In bees, for example, the molecular mechanisms mediating feeding and maternal care converge on the insulin pathway (Toth and Robinson, 2007), and modifications of this pathway lead to shifts from solitary to eusocial lifestyles at evolutionary timescales, as well as developmental shifts from nursing to foraging behavior.

Studies in bees also provide evidence for the evolution of social behavior from feeding circuits both directly and indirectly via parental care. Evidence for the involvement of NPY in grouping behavior in *C. elegans* and *Drosophila* suggests that this particular feeding circuit was co-opted in the evolution of social behavior well before and independently of the evolution of parental care, at least in invertebrates. In contrast, differences in insulin signaling and the expression of vitellogenin suggest that maternal behavior has indeed acted as an evolutionary intermediate to the evolution of social behavior from foraging/feeding mechanisms in bees, as appears to be the case in many vertebrates and at least some insects. Comparative studies linking the neural and molecular mechanisms of feeding, parental care and social behavior will help to elucidate the prevalence of these alternative evolutionary trajectories.

Finally, repeated targeting of feeding pathways during independent evolutionary transitions to eusociality as well as developmental behavioral transitions within eusocial societies has given rise to the idea that molecular pathways involved in nutritional

state and feeding behavior act as a ‘toolkit’ for the evolution and maintenance of eusociality in insects (Ament et al., 2008). We suggest that the modification of neural and molecular components important in feeding behavior may be taxonomically much more broad and targeted in the evolution of social behavior across animals. While work in vertebrates addresses connections between feeding behavior and social behavior at both the level of molecular mechanisms and neural circuits (see above), work in social insects is largely limited to the molecular level. Additional work is necessary to explore the extent to which neural circuits regulating feeding and social behavior are overlapping in invertebrates and how these relate to patterns in vertebrates. These findings will be of particular comparative interest given the ongoing debate about deep homology in the neural circuits underlying behavior across vertebrates and invertebrates (Rittschof and Robinson, 2016).

Conclusions

We have reviewed how evolutionary innovations in social behavior, including parental care and eusociality, have evolved through modifications of molecules and neural circuits mediating feeding and foraging behavior. Given that diverse forms of parental care and other types of social behavior have evolved independently across taxa, it is remarkable that largely conserved molecular mechanisms and brain regions appear to link feeding and social behavior across highly divergent animal lineages. It is unclear with our current knowledge how the neural circuits of feeding and social behavior function together, as nutritional state could gate reproductive behavior or the two neural circuits could be reciprocally inhibitory or facultative depending on the species and circumstance. More research at the neural circuit level is needed to disentangle these and other possibilities. We suggest connections between feeding/foraging circuits and social behavior are evolutionarily ancient and provide fertile ground for research examining behavioral evolution.

Molecular mechanisms mediating nutritional state and feeding behavior have already been proposed as a molecular toolkit for the evolution of eusociality (Ament et al., 2010), and we review evidence that the connections between feeding and sociality are in fact evolutionarily much more widespread. Broad-scale comparative studies examining connections between feeding behavior, social behavior and their underlying mechanisms will continue to be particularly valuable in identifying shared principles underlying the evolution of complex social behavior. Moreover, comparative studies will help to distinguish the unique mechanistic characteristics that provide variations on this theme. For example, the NPY/NPF pathway appears to be manipulated in different ways in various social contexts, where the NPY/NPF peptide is upregulated during honey bee maturation into foragers and hyperphagia (increased feeding) in parental ring doves and lactating mammals. In contrast, the NPY/NPF receptors are upregulated during parental care in mouthbrooding cichlids and downregulated in parental burying beetles. Comparative approaches will determine whether these differences represent signatures of shared evolutionary history, are linked to particular behavioral strategies or represent modifications of alternative pathway components that nonetheless generate similar behavioral outcomes.

In addition to comparative studies, experimental manipulations at both the behavioral and molecular level are necessary. Studies explicitly examining the influence of nutritional state on parental and social behavior will more definitively identify causal relationships between feeding and social behaviors (Frommen et al., 2007). Similarly, direct manipulations of circuits and

molecules must be expanded beyond current model systems to include a greater diversity of taxa representing a wider range of ecologies, life histories and care strategies. Fortunately, ongoing technological advances are making these types of manipulations increasingly feasible outside of traditional model systems, facilitating bridging of the gap between ecological and neurobiological work. In concert, these approaches will further our understanding of how general principles are modified to fine tune behavioral switches in species with distinct life histories, care strategies and nervous systems. Ultimately, this work will contribute not only to our understanding of the modification of neural and molecular feeding pathways in the evolution of social behavior, but to the fundamental question of how evolution builds upon existing substrates to give rise to increasingly complex behavioral systems.

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Competing interests

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