

REVIEW

A neuroendocrine perspective on the origin and evolution of cooperative breeding

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ABSTRACT

Cooperative breeding behavior in birds ranges from inducible to obligate strategies and has evolved across diverse taxa, in species that display a wide range of social and reproductive behavior. It is often thought to evolve when independent breeding is constrained, and cooperation increases fitness. Yet many systems show variable, even maladaptive, fitness effects. This observation, together with the wide range in the form and frequency of cooperative breeding, raises the question of how the recurrent appearance of cooperative breeding and its extensive variation across species—from inducible to obligate—can be explained. Here, we take a proximate perspective on the evolution of cooperative breeding to argue that cooperative strategies are delineated by the history of prior adaptations and emerge through the rearrangement of preexisting neuroendocrine mechanisms underlying social, dispersal, and parental behaviors. Natural selection sorts among the resultant variants to alter regulation of cooperation, producing stabilization through either greater developmental entrenchment or greater reliance on environmental cues. Thus, species showing inducible cooperative behavior may be at a transitory stage in this process. To assess this possibility, we first evaluate evidence that the components of cooperative breeding are common across taxa. Then, we review the neuroendocrine mechanisms that regulate the pathways underlying cooperative strategies. Finally, we assess the evidence for neuroendocrine linkages during development that may channel coexpression of some components of cooperative breeding and facilitate its evolution. We conclude that understanding the mechanistic bases of the behaviors comprising cooperative breeding strategies may provide novel insight into the recurrent emergence of this strategy across disparate environments and avian taxa.

Keywords: behavior, evolution, genetic accommodation, helpers, plasticity, social behavior network

LAY SUMMARY

- Cooperative breeding behavior involves 3 or more birds working together to raise young.
- It has evolved across a diversity of avian taxa and there is a wide range in how often it is expressed within species.
- How can the recurrent appearance of cooperative breeding and its extensive variation across species be explained?
- Here, we take a proximate perspective to argue that cooperative strategies appear because the behaviors comprising cooperative breeding are common, and the neuroendocrine mechanisms underlying these behaviors can be easily linked.
- Recent discoveries in neuroscience show that connections in the brain between neurons that regulate social behavior, parental care and dispersal are ancestral to birds and so this pre-existing network may facilitate the appearance of cooperative breeding across taxa.
- Understanding the mechanistic bases of cooperative breeding provides new insight into its evolution and provides a framework to explain the breadth and diversity of cooperative strategies.

Una perspectiva neuroendocrina sobre el origen y la evolución de la cría cooperativa

RESUMEN

El comportamiento de cría cooperativa en las aves varía entre estrategias inducibles a obligadas y ha evolucionado a través de diversos taxones, en especies que despliegan un amplio abanico de comportamientos sociales y reproductivos. Usualmente se piensa que evoluciona cuando la cría independiente está restringida y la cooperación aumenta la adecuación biológica. Aun así, muchas especies muestran efectos variables, e incluso maladaptativos, en la adecuación biológica. Esta observación, junto al amplio abanico de formas y frecuencias de la cría cooperativa, plantea la pregunta sobre cómo la aparición recurrente de cría cooperativa y su gran variación entre especies—de inducible a obligada—puede ser explicada. Aquí, tomamos una perspectiva aproximada sobre la evolución de la cría cooperativa para

argumentar que las estrategias cooperativas están delineadas por la historia de las adaptaciones previas y emergen a través del reordenamiento de mecanismos neuroendocrinos preexistentes subyacentes a los comportamientos sociales, de dispersión y parentales. La selección natural opera entre las variantes resultantes para alterar la regulación de la cooperación, produciendo estabilización a través de una mayor consolidación del desarrollo o una mayor dependencia de las señales ambientales. De este modo, las especies que exhiben un comportamiento de cooperación inducible pueden ser un estado transitorio en este proceso. Para evaluar esta posibilidad, primero evaluamos la evidencia de que los componentes de la cría reproductiva son comunes a través de los taxones. Luego, revisamos los mecanismos neuroendocrinos que regulan los circuitos que subyacen a las estrategias cooperativas. Finalmente, evaluamos la evidencia de vínculos neuroendocrinos durante el desarrollo que puedan canalizar la co-expresión de algunos componentes de la cría cooperativa y facilitar su evolución. Concluimos que la comprensión de las bases mecanicistas de los comportamientos que comprenden las estrategias de cría cooperativa puede proporcionar una nueva perspectiva sobre la aparición recurrente de esta estrategia en ambientes y taxones de aves dispares.

Palabras clave: acomodación genética, ayudantes, comportamiento, evolución, plasticidad, red de comportamiento social

INTRODUCTION

Cooperative breeding behavior, in which 3 or more individuals collectively raise young in a single reproductive event (Koenig 2017), ranges from inducible parental behavior expressed toward the offspring of others (e.g., when noncooperative species exhibit cooperative breeding when placed in captivity; Skutch 1987), to obligate strategies where successful reproduction does not occur without cooperation (e.g., in White-winged Choughs [*Corcorax melanorhamphos*], Heinsohn 1991). Phylogenetic studies indicate that it has evolved independently at least 28 times, with upwards of 35 families showing repeated gains and losses of cooperative breeding (Cornwallis et al. 2010, 2017). Although many phylogenetic studies treat cooperative breeding as a dichotomous trait, noting its presence or absence in a particular taxon (but see Riehl 2013), this approach ignores the extensive variation across species in both its frequency and variability of expression. In fact, in the majority of cooperatively breeding species, <10% of individuals within a population display it (Cockburn 2006). Moreover, as a consequence of evolving in species with diverse natural histories, cooperative breeding incorporates a wide range of phenomena, from nonbreeding offspring aiding their parents to polygynandrous societies of unrelated individuals engaged in group offspring care (Riehl 2013). It is apparent that what has previously been described as a single phenomenon has arisen from a bewildering array of historical points (Cornwallis et al. 2010); yet, when cooperative breeding appears, it is comprised of similar behaviors, including social, parental, and dispersal behaviors.

Traditionally, there has been a focus on the ecological contexts that favor evolution of cooperative breeding. Yet, this approach has been largely unsuccessful in identifying consistent environmental correlates; indeed, across studies, the evolution of cooperative breeding has been associated with both benign and harsh environments, as well as both variable and stable habitats (Emlen 1982, Koenig and Dickinson 2004, Rubenstein and Lovette 2007, Hatchwell

2009). In general, cooperative breeding is thought to evolve when there is a constraint on the ability of new recruits entering a population to reproduce independently. However, constraints on breeding are nearly ubiquitous in nature, yet cooperative breeding is relatively rare compared to other strategies (Cockburn 2006), suggesting that the repeated emergence of cooperative breeding cannot be explained by ecological context alone. Moreover, Jamieson (1989) questioned the idea that helping behavior is a product of natural selection. Instead, he proposed that, while communal living may be a target of selection, helping behavior may simply emerge once communal living has evolved without natural selection necessarily favoring its expression. The idea that cooperative breeding is emergent has been supported by the fact that, in many cooperative breeders, there are no clear reproductive or survival benefits of having or being a helper (Dunn et al. 1995, Double and Cockburn 2003, Potticary et al. 2016, Potticary and Duckworth 2018). As such, adaptive explanations are often used for species where a fitness benefit has been demonstrated, while the emergent explanation is invoked when no fitness benefits have been found. Thus, on one end of the spectrum, cooperative breeding is viewed as a unique strategy that evolves through natural selection as a distinct trait, and at the other end of the spectrum, cooperative breeding is viewed as an emergent property of group living that is not necessarily a target of natural selection. However, viewing cooperative breeding as either adaptive or not adaptive precludes a synthesis that explains how and why cooperative breeding may exist as both an epiphenomenon and as a finely tuned strategy.

Here, we propose a third possibility: that each of these views is correct to some extent and rather than representing alternatives, they represent distinct phases in the evolution of cooperative breeding. Under this view, helping behavior does not always have to be adaptive, as it first appears as an epiphenomenon that emerges when a non-helping species encounters atypical environmental circumstances. Over time, if the environment that induces it becomes more common, perhaps through evolutionary

changes in dispersal or affiliative behavior, it could lead to more frequent expression of helping behavior and provide the opportunity for selection to refine strategies within a population, such that they become either developmentally entrenched or more sensitive to a particular environmental context. For example, in taxa that have experienced group living for a long evolutionary time, there may be evolutionary changes in the threshold for expressing helping behavior, to the point that all individuals in the population show the behavior (e.g., in White-winged Choughs [Heinsohn 1991](#)). Whereas, in other taxa, facultative expression—or existence of multiple alternative behavioral strategies, of which cooperative breeding is one—may be a distinct evolutionary endpoint, such that cooperative breeding is expressed in response to specific environmental cues. Overall, the process of evolving from emergent variation to greater developmental entrenchment is broadly known as genetic accommodation ([West-Eberhard 2003](#)).

Testing alternative hypotheses for the origin of cooperative breeding is difficult because all 3 views (i.e. traditional, emergent, and genetic accommodation) predict that cooperative breeding behaviors should be observed in particular habitats—under the traditional view, this is because the strategy is adaptive and has been favored by the unique selection pressures imposed by that habitat type. Whereas, under genetic accommodation and the emergent view, behavior emerges in some habitats because it is directly induced by those habitats, even in the absence of selection for its expression. Thus, habitat association studies are not useful in differentiating these hypotheses; however, each hypothesis makes alternative predictions about the underlying proximate mechanisms of cooperative breeding across species ([Table 1](#)). As such, a greater understanding of the neuroendocrine basis of cooperative breeding can enable us to distinguish between these alternatives and provide new insight into its evolution.

Behavior is the final outcome of many underlying neurobiological processes that integrate information about current context and internal organismal state. Sensory information is processed in the brain by cognitive, motivation, and emotion circuits that, in turn, influence the decisions an individual can make. Various control centers gather and process environmental information and regulate behavioral responses to both internal and external cues. The neuroendocrine system produces hormones, which are chemical messengers that bind to receptors across the brain and body, coordinating whole-organism responses to stimuli. Mechanisms that impact multiple behaviors essentially form a “link” between them, which ensures the coexpression of these behaviors. For example, testosterone has been found to simultaneously stimulate mating behaviors and aggression ([Ketterson et al. 1992](#), [Wingfield et al. 2001](#)), but is antagonistic to parental care,

thus making these behaviors linked hormonally ([Ketterson et al. 2009](#)). Importantly, the flexibility of a behavior will depend on the type of neuroendocrine linkage, the timing of its development, and whether it is reversible. This spectrum of flexibility is often categorized into organizational and activational effects, although these are seldom discrete categories in practice ([Arnold and Breedlove 1985](#)). Organizational effects occur early in development and have lasting, potentially permanent, effects on later behavior (such as the effects of early stress on brain development; e.g., [Liu et al. 1997](#), [Meaney and Szyf 2005](#)), whereas activational effects are transient and can promote reversible behavior throughout the lifetime of an individual (e.g., the seasonal effect of hormones on the expression of parental care behavior; [Arnold and Breedlove 1985](#)). Thus, the breadth of neuroendocrine mechanisms and their ability to link behaviors vary in their flexibility over the lifetime of an individual, with implications for behavioral evolution.

Cooperative breeding is an illustrative example of such behavioral coordination, as it often requires the simultaneous coexpression of reduced dispersal (e.g., when individuals remain near parents to help), increased affiliative behavior toward individuals that are not mates, and motivation to provide parental care to offspring that are not one's own. Coexpression, by definition, requires a linkage between each behavior, such they are expressed together—for example, this may be due to a habitat that produces simultaneous expression of each behavior, or an evolved, mechanistic neuroendocrine linkage. The traditional, emergent, and genetic accommodation hypotheses make alternative predictions about the timing, development of, and the structure of the links between the neuroendocrine mechanisms that allow for coexpression of cooperative breeding behaviors ([Table 1](#)). First, the traditional view inherently predicts that the component behaviors that comprise a behavioral strategy are ontogenetically independent of each other, and thus available to form new associations when selection favors them. Under the traditional view, we would expect neuroendocrine linkages among components of a behavioral strategy only if they are favored by selection (i.e. only in species that have already evolved cooperative breeding) with no linkages present in species that have not evolved cooperative breeding. On the other hand, the genetic accommodation hypothesis does not assume ontogenetic independence among cooperative breeding behaviors. Instead, the emergence of cooperative breeding may be enabled by preexisting neuroendocrine links between the affiliative, parental, and dispersal behaviors, such that a change in the mechanisms underlying one behavior may impact expression of others. Such links may facilitate the rapid appearance of cooperative breeding, even in species

TABLE 1. Predictions of alternative hypotheses for origin of cooperative breeding.

Hypotheses	Neuroendocrine links between cooperative breeding components	Developmental timing of neuroendocrine basis of cooperative behavior
Emergent	Present in all birds	Late in development (activational)
Traditional	Present only in species that already show cooperative breeding	Early in development (organizational)
Genetic accommodation	Present in all birds	Developmental timing depends on history of expression within a clade: clades with a longer history of expressing cooperative phenotypes should show earlier developmental timing than clades in which cooperative breeding is only recently expressed

that do not typically show cooperative behavior, and further explain the recurrent appearance of cooperative breeding across disparate avian taxa.

Associations between integrated, or functionally linked, traits are often thought to arise early in development, to ensure that all components are expressed together appropriately (Cheverud 1996, West-Eberhard 2003). Thus, each hypothesis makes alternate predictions about the timing of when linkages between cooperative behaviors form and the frequency that cooperative breeding is expressed within species. The traditional view predicts that all cooperatively breeding species, irrespective of how frequently the strategy occurs within a species, have evolved neuroendocrine linkages in the brain to ensure the expression of cooperative breeding relative to the selective context. The emergent view predicts that cooperative species, even obligate cooperators, do not form neuroendocrine differences in ontogeny; instead, coexpression of cooperative behaviors occurs through activation of adult neuroendocrine structures. The genetic accommodation hypothesis predicts that, across species, there should be variation in when associations between cooperative behaviors develop that is correlated with how frequently cooperative breeding is expressed within species. Specifically, we expect that, in obligate cooperative breeders, the proximate neuroendocrine mechanisms that underlie cooperative breeding behavior should arise earlier in development compared to either noncooperative or facultative species. Thus, our perspective makes specific predictions that can only be tested by assessing the development and neuroendocrine mechanisms of cooperative breeding from a comparative perspective.

Our goal in this review is to provide a synthesis of what is known about the neuroendocrine mechanisms of the components of cooperative breeding (e.g., parental care, grouping behavior, and dispersal), for which there is a substantial body of work, and to synthesize this field to construct a framework that can guide future comparative studies of neuroendocrine mechanisms of cooperative breeding that can illuminate evolutionary processes. We first identify the behaviors comprising cooperative

breeding and show that these behaviors are common and often linked, not just in birds, but across all vertebrates. We then review evidence for the variable timing of the developmental associations underlying the components of cooperative breeding. Finally, we conclude with suggestions for future experimental work on how the neuroendocrine mechanisms underlying cooperative breeding vary across species in relation to their prevalence and history of cooperative breeding.

COOPERATIVE BREEDING REQUIRES COEXPRESSION OF COMMON BEHAVIORS

Cooperative breeding has evolved across diverse avian taxa yet remains a relatively rare strategy (Cockburn 2006). However, while rare as a breeding strategy (Cockburn 2006), it is comprised of social and breeding behaviors that are commonly expressed across Aves. Specifically, the behaviors comprising cooperative breeding include parental care, affiliative behavior, and philopatry. The only difference in cooperative breeders is that these behaviors are combined in a specific, correlated manner, where individuals show parental care toward offspring that are not their own and form close and long-lasting relationships with individuals that are not mates (Koenig and Dickinson 2004).

Parental care exhibited in a cooperative context can include nest construction, incubation of eggs, mate feeding, nest defense, brooding, and feeding chicks—all of which are general parental behaviors expressed across Aves, only, in this case, they are expressed by a nonparent. For example, even though helpers in birds are often males, parental behavior by males is not unique to cooperative breeding; indeed, paternal care is more common among birds than any other vertebrate class, with biparental care exhibited in more than 80% of avian species (Cockburn 2006). Further, cooperative breeding, at minimum, requires the formation of a group of 3 or more individuals of which only 2 are typically mates. Stability of such groups requires prosocial activity, bonding, and attribution of positive or negative qualities to social stimuli. Like parental care, group

formation, such as foraging and seasonal flock formation, is common across avian taxa, suggesting that affiliative behavior may often predate the expression of cooperative breeding. Lastly, as most cooperative breeding systems involve young aiding family members in subsequent breeding attempts, it is broadly recognized that philopatric behavior is an important facet (Cockburn 2003, Griesser et al. 2017). Male-biased philopatry is common in birds, even in species that do not display cooperative breeding (Greenwood 1980, Hatchwell 2009). Thus, all behaviors coexpressed in a cooperative context are also commonly expressed in noncooperative contexts.

For this reason, it is likely that all components of cooperative breeding are preexisting within populations, and cooperative breeding emerges when these behaviors are expressed in a new combination, outside of their usual context (Jamieson 1989). Support for this idea comes from the observation that cooperative breeding can appear rapidly when noncooperative species are placed in captivity (Skutch 1987). This suggests that the potential to express cooperative breeding behavior exists in all birds which display parental care and what varies across species is how entrenched the coexpression of the components of cooperative breeding are in normal development (i.e. the extent to which initially emergent behavioral variation has come under greater developmental control). Importantly, as we discuss below, the neuroendocrine mechanisms underlying the components of cooperative breeding behavior often overlap developmentally, and such overlap may facilitate the emergence of cooperative breeding in novel conditions.

NEUROENDOCRINE LINKAGES AMONG COMPONENTS OF COOPERATIVE BREEDING BEHAVIORS

Cooperative breeding is comprised of multiple independent types of behavior (e.g., affiliative, dispersal, and parental care) expressed together relative to a particular context. Given that these behaviors are common across birds, understanding the properties and links between the neuroendocrine mechanisms that underlie the different behaviors composing cooperative breeding is key to testing alternative hypotheses about its emergence and evolution (Table 1). What properties of neuroendocrine structure can produce rapid emergence of cooperative behavior on ecological timescales? While there has been very little work explicitly addressing this question in birds, it is known that a network of brain areas underlying variation in social behavior are ancestral to vertebrates (Banerjee et al. 2017). Therefore, we draw on examples across vertebrates to assess what is known about the neuroendocrine basis of the key behavioral components

of cooperative breeding, while taking particular care to highlight studies in birds and synthesize this literature to provide a road map for future comparative work in avian taxa.

Recent studies have identified a set of areas within the forebrain and midbrain that is homologous across vertebrates (see O'Connell and Hofmann 2011, Goodson and Kingsbury 2013; Figure 1) and that regulates multiple social behaviors including aggression, affiliation, bonding, parental behavior, and responses to social stress (Goodson 2005, Goodson and Thompson 2010). The conserved core of this "social behavior network" connects to other pathways related to social memory formation and reward circuitry, such as the dopaminergic pathway (e.g., Young and Wang 2004). The nodes of the social behavior network are reciprocally connected and contain receptors for sex steroid hormones and nonapeptides (Goodson 2005) both of which are known to modulate social behavior. Switches between behavioral phenotypes may be enabled by changes in the "weights" of connections between the nodes, due to variation in receptor density, type, and distribution as well as neuron number, cell activation, or a combination of these elements, providing a diversity of targets for behavioral regulation and evolution (Goodson 2005, Goodson et al. 2006, Soares et al. 2010). Soares et al. (2010) point out that different combinations of activation across these nodes can vary at multiple levels (e.g., within individuals over time due to current experience) as well as among individuals and species due to either genetic differences or the early-life developmental environment. This is important, as the evolution of cooperative breeding from emergent variation in adults to developmentally entrenched strategies (i.e. one potential outcome of genetic accommodation), requires a neuroendocrine system that can produce behavioral correlations activationally in adults, and also allow for the evolution of earlier developmental linkage (e.g., organizational) if selection favors their coexpression.

Conservation of the social behavior network across vertebrates, together with flexibility in how it is activated in adult organisms and organized during development (O'Connell and Hofmann 2011), suggest that cooperative breeding has arisen so many times in birds because the behavioral components that comprise it are not ontogenetically independent. While the details of how the social behavior network functions are not fully known, it is clear that neuroendocrine components of this network overlap in their effects on the expression of behaviors that produce cooperative breeding. The traditional view of cooperative breeding inherently assumes that behaviors composing cooperative breeding are independent, such that individuals modulate behavioral coexpression optimally relative to the context that selects for it. However, such an overlap among neuroendocrine components of cooperative behavior may

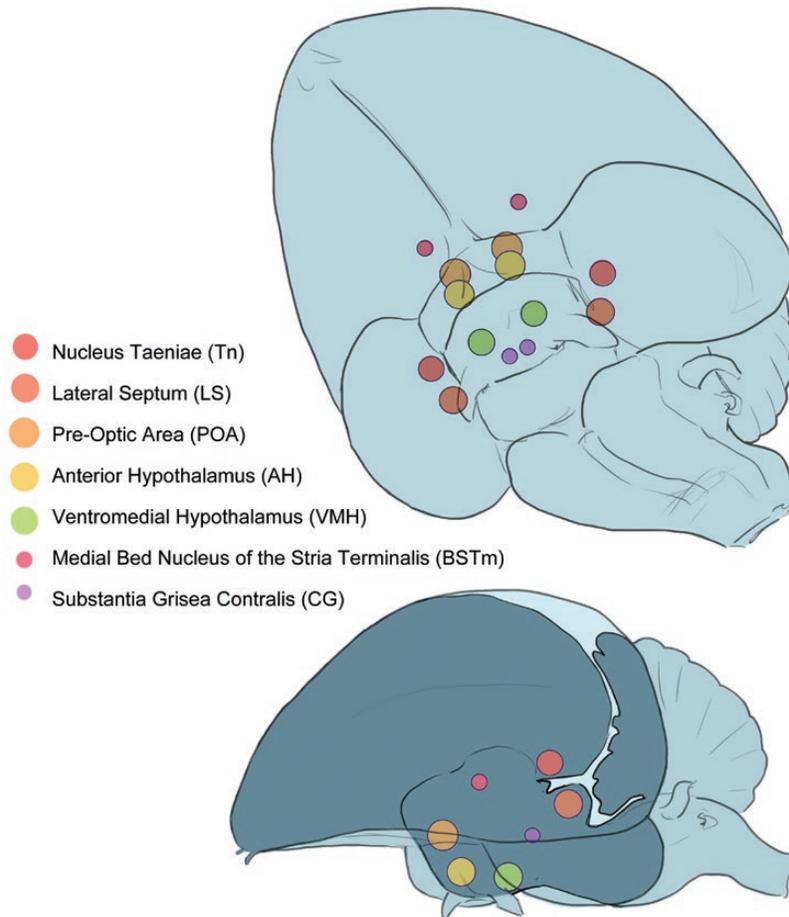


FIGURE 1. Nodes of the core social behavior network in birds. Brain regions were identified per [Goodson and Kingsbury \(2013\)](#) and [O'Connell and Hofmann \(2011\)](#).

indicate that changes in one component can influence other components, such that some strategies are more likely to form than others. In the next section, we explore how such links between cooperative breeding behaviors may occur during both adulthood (leading to rapid emergence of cooperative behavior) and during early ontogeny (leading to developmental entrenchment).

REGULATION IN ADULTHOOD: ACTIVATIONAL LINKAGES WITHIN THE SOCIAL BEHAVIOR NETWORK

The emergence of cooperative breeding requires that coexpression of cooperative breeding behaviors can happen rapidly, or from a neuroendocrine perspective, can be produced through activation of preexisting neuroendocrine structures. If the mechanisms that influence the expression of cooperative behaviors overlap, it is possible that such shared regulation of these behaviors can produce the rapid emergence of cooperative breeding behavior in adults, without requiring the behavior to be adaptive ([Table 1](#)). Behavior is regulated in adults by the activational

effects (i.e. having a generally transient or reversible effect) of nonapeptides and hormone systems, which often overlap in the behaviors that they influence. Here, we review well-studied neuroendocrine systems that “link” the behaviors comprising cooperative breeding strategies in adult organisms.

Nonapeptides Influence Both Group Formation and Parental Care

The nonapeptides oxytocin and vasopressin and their homologues (mesotocin and arginine vasotocin in birds, respectively) are part of an ancient family of conserved peptides that have existed for over 700 million years ([Donaldson and Young 2008](#), [Banerjee et al. 2017](#)) and are extensively expressed in the social behavior network, enabling them to modulate the network's response to various stimuli and behavioral outputs. These nonapeptides influence the regulation of social behaviors pertinent to cooperative breeding across vertebrates ([Soares et al. 2010](#)). Indeed, their effects can be very similar across taxa: administering mammalian oxytocin to amphibians and

isotocin from fish to mammals can produce similar territorial behaviors (Venkatesh et al. 1997, Ten Eyck and Ten Eyck 2017). As the role of these nonapeptides in cooperatively breeding birds has not been tested explicitly, we include studies from across vertebrates, yet use the nomenclature for the avian homologues mesotocin and vasotocin throughout.

Mesotocin and vasotocin circuits arise from neurons of the preoptic area and hypothalamus of all vertebrates (Kelly et al. 2011), and projections from nonapeptide cell groups innervate the core social behavior network (Goodson 2013). Higher levels of mesotocin can increase prosocial motivation (Goodson et al. 2012b), trust within a group (humans; Kosfeld et al. 2005), and enhance sensitivity to social stimuli (Young and Wang 2004), increasing in-group bias and dissociation from other groups (De Dreu 2012, Mustoe et al. 2015). Mesotocin is broadly thought to influence affiliative behavior across reproductive and nonreproductive contexts (Goodson and Thompson 2010). For example, seasonally flocking sparrows show a winter increase in mesotocin activity; however, this was not observed in a closely related non-flocking species (Goodson et al. 2012b). Vasotocin has similar effects, although its receptors and expression levels vary across structures and the effects of mesotocin and vasotocin are often sex-specific even when producing the same behaviors (Goodson and Thompson 2010). Vasotocin regulates social recognition (Everts and Koolhaas 1999), social valence (i.e. the degree of attraction or aversion shown toward others; Goodson and Wang 2006), parental behavior (Lynn 2016), and can influence multiple types of grouping behavior. Studies show that flocking bird species generally have more vasotocin binding sites in the lateral septum than territorial species (Goodson et al. 2006), knockdown of vasotocin production in the medial bed nucleus of the stria terminalis decreases gregariousness within social species (Kelly et al. 2011), and gregarious estrildid species have ~10× the number of vasotocin neurons in the medial bed nucleus of the stria terminalis than less social species (Goodson and Wang 2006). Thus, nonapeptides regulate multiple components of cooperative breeding (see Table 2 for full summary), and this makes it likely that they are important in the regulation of helping behavior as well.

Not only do vasotocin and mesotocin influence social behavior, but they can also increase attraction or aversion to stimuli through selective activation of the hypothalamic–pituitary–adrenal (HPA) axis, amygdala, and basal forebrain reward system (Soares et al. 2010) suggesting that stress and the social behavior network are intimately linked. Mesotocin can inhibit both basal and stress-induced HPA axis activity (Neumann et al. 2000, Kirsch et al. 2005) and reduce anxiety-like effects associated with social stimuli. This can create a feedback where increased social

interactions decrease HPA axis activity, possibly creating a mechanism by which helping behavior can emerge in novel (and presumably stressful) situations. Further evidence of the link between these nonapeptides and the HPA axis comes from seasonally flocking birds, which show a winter increase in mesotocin and corticotropin-releasing hormone innervation into the lateral septum (Goodson et al. 2012b). In contrast to the inhibitory effects of mesotocin, vasotocin acts synergistically with corticotropin-releasing hormone to activate the HPA axis (Wingfield 2013), and is often associated with social anxiety (e.g., Beery et al. 2008). Overall, nonapeptides are crucial in modulating feedback between stressors and social interactions in a variety of life history stages and contexts.

HPA axis activation also influences parental care (Bole-Feysot et al. 1998, Angelier et al. 2009). While an intense stress response generally results in abandonment of breeding activities (Wingfield and Sapolsky 2003), moderate elevation of corticosterone can enhance parental behavior (see Lynn 2016 for a review). The mechanisms by which corticosterone may increase parental care are not well understood, but it is possible that it may increase an individual's sensitivity to begging cues while mobilizing energy reserves because of broad corticosterone action (e.g., Kitaysky et al. 2001). Most importantly, these links between HPA axis response, nonapeptides, and parental behavior mean that social harmony, low HPA axis activity, and high parental care are likely to feedback on one another. As further evidence of this, there are reciprocal interactions between neurons that contain corticotropin-releasing factor and mesotocin in the hypothalamus, suggesting interdependent regulation of the two (Dabrowska et al. 2011). During an HPA axis stress response, while vasotocin acts synergistically with corticotropin-releasing factor to increase the stress response, mesotocin acts to dampen it. Thus, there is the potential for both positive and negative feedbacks between stress and social interactions depending on which of these effects dominate. Disentangling how these feedbacks work is an important topic for future research and may shed light on how cooperative behaviors can emerge in typically noncooperative species under novel conditions.

Finally, depending on the context and the species, vasotocin can influence social behavior in both positive and negative ways. For example, increasing the density of vasotocin receptors in the pallial regions of voles increased affiliative behavior (Pitkow et al. 2001), whereas experimentally disabling vasotocin production in finches inhibited affiliative behavior while simultaneously increasing aggression (Kelly and Goodson 2014). Moreover, the mechanisms of sociality and aggression often overlap across taxa, such that more sociable individuals are often less aggressive (see Kelly and Vitousek 2017 for a review).

TABLE 2. Neuroendocrine mechanisms modulating cooperative breeding behaviors often influence more than one behavior. Components refer to aspects of cooperative breeding strategies and behavior denotes specific behaviors affiliated with each component. Recipient refers to either the individuals toward which each behavior is performed, or performed with, if it is a group activity (G = group, P = reproductive partner, F = flock, O = offspring). Neuroendocrine modulators are nonapeptides and endocrine factors that have been shown to be associated with each behavior (AVT = arginine vasotocin, CRH = corticotropin-releasing hormone, MT = mesotocin, PRL = prolactin, VIP = vasoactive intestinal peptide, T = testosterone, BSTm = bed nucleus of the stria terminalis, LS = lateral septum, POA = preoptic area, PVN = paraventricular nucleus, AH = anterior hypothalamus). Brain regions are the regions/projections known or putative locations that influence each social behavior.

Components	Behaviors	Recipient	Neuroendocrine modulators	Brain regions	References
Grouping	Affiliation	G, P, F, O	AVT, CRH, MT, PRL, VIP	Amygdala, forebrain reward system, BSTm, LS, midbrain, POA, PVN	1, 2, 3, 4, 5, 6, 7, 8, 9
	Valence				
	Bonding				
	Recognition				
	Perception				
Parental care	Aggression	G, P, O	AVT, CRH, MT, T, VIP	AH, amygdala, BSTm, LS, POA	8, 10, 11
	Nest building	G, P	AVT, CRH, MT, PRL, T, VIP	Amygdala, forebrain reward system, BSTm, LS, midbrain, POA	6, 9, 12, 13, 14
	Incubation	O	T, VIP		
	Feeding	G, P			
	Brooding	O			
Dispersal	Stimulus salience ^a	G, P, O			
	Exploration Activity	G, P	CRH	Amygdala	15

^aAn organism's sensitivity to different stimuli.

References: 1. Kingsbury and Goodson (2014); 2. Everts and Koolhaas (1999); 3. Festante et al. (2020); 4. Goodson and Wang (2006); 5. Goodson et al. (2012a); 6. Hammock and Young (2005); 7. Kingsbury (2015); 8. Kelly and Goodson (2014); 9. Bole-Feysot et al. (1998); 10. Lopatina et al. (2011); 11. Goodson et al. (2012b); 12. Kingsbury et al. (2015); 13. Ketterson et al. (1992); 14. Champagne et al. (2003); 15. Hau and Goymann (2015).

This link between the two could help explain why facultative cooperative breeders often show distinct alternative strategies where less aggressive individuals are the most likely to help (e.g., Potticary and Duckworth 2018).

Prolactin and Vasoactive Intestinal Peptide Influence Parental Care and Social Behavior

The preoptic area of the brain is a key node of the social behavior network and has long been thought to mediate variation in parental care across vertebrates (Buntin 1996, Champagne et al. 2003), with some degree of regulation occurring due to the peptide hormone prolactin. Prolactin is secreted by the anterior pituitary and has been related to expression of male parental care in 25 avian species across 9 orders (Schradin and Anzenberger 1999). Prolactin is often positively correlated with parental behaviors such as incubation, brooding, and feeding of offspring (Bole-Feysot et al. 1998, Lynn 2016), including in cooperative species. For example, helpers of two cooperatively breeding jay species demonstrated an increase in prolactin prior to the presence of offspring, which was not observed in nonbreeding individuals of a closely related jay species (Schoech et al. 1996, Brown and Vleck 1998). Yet, the relationship between prolactin and helping is unclear. While high levels of circulating prolactin may be required for parental care, species often

vary in the degree to which reproductive stimuli and prolactin responses are integrated, and prolactin levels do not necessarily correlate with the degree of care across avian species. For example, elevated prolactin occurs in species that do not show parental care (Dufty et al. 1987), and prolactin is sometimes linked more strongly to other cues, like photoperiod, than it is to nesting (see Lynn 2016, Williams 2012 for reviews), concomitant with its involvement in a vast number of metabolic and physiological processes (Freeman et al. 2000). This may reflect variation in the distribution of prolactin receptors, which have been found in numerous areas in the brain including the preoptic area, hypothalamus, and pituitary (Bole-Feysot et al. 1998). For these reasons, it has been argued that prolactin may primarily serve to promote attention to breeding activities by increasing the attractiveness of offspring cues (i.e. prolactin changes perception of when it is appropriate to show breeding behavior; Smiley 2019). However, whether prolactin elevation directly mediates an increased response to the presence of breeding stimuli (e.g., the presence of chicks or reproductively active group members), or precedes helping behavior in cooperatively breeding species, is unclear.

Prolactin is primarily stimulated by vasoactive intestinal peptide in birds (Vleck and Patrick 1999), and vasoactive intestinal peptide receptors are distributed

throughout the social behavior network. This distribution is unsurprising: functional associations between mechanisms of grouping behavior and parental care are necessary because parental care in birds almost always requires, at minimum, affiliation between parent and offspring. It has been broadly hypothesized that the neurobiological processes underlying parental, particularly paternal, behavior are integrated with the mechanisms that promote social behavior more generally (Fernandez-Duque et al. 2009). Indeed, vasoactive intestinal peptide mRNA and transcriptional activity associated with nest building behavior were found in nearly every node of the social behavior network (Kingsbury et al. 2015). This distribution likely accounts for why vasoactive intestinal peptide has also been shown to be important for other social behaviors, such as aggressive and agonistic communication, gregariousness, and pair-bonding (Kingsbury and Goodson 2014), as well as influencing parental care behavior (Badyaev and Duckworth 2005). Ring doves that were allowed to freely associate with their young vs. only seeing them through wire mesh showed increased neuronal activity in the preoptic area, medial bed nucleus of the stria terminalis, and lateral septum, indicating that contact with offspring stimulates multiple regions of the social behavior network and parental care behavior simultaneously (Buntin et al. 2006). As both parental care and group formation require affiliation, it is possible that changes in the mechanisms producing both types of affiliation (e.g., vasoactive intestinal peptide) may influence the likelihood of individuals showing a heterochronic shift in parental care behavior, enabling the emergence of helping behavior on short timescales. However, the relationship between vasoactive intestinal peptide and both the proximate and ultimate expression of cooperative breeding behaviors is unknown and warrants future research.

Individual Variation in Dispersal Tendency Associated with Personality Variation

Young individuals that do not have an opportunity for independent breeding can stay, help, and queue for a breeding position, float in the natal population, or disperse to breed independently (Kokko and Ekman 2002). Recent phylogenetic work indicates that formation of family-based groups often precedes the appearance of cooperative breeding (Griesser et al. 2017). Most cooperative breeding systems involve young remaining philopatric and aiding their parents in subsequent nesting attempts. Because young birds almost always remain with parents in a post-fledging group for some period of time thus, a transition from the post-fledging groups commonly observed across avian taxa to longer-term groups primarily requires an extension in the length of affiliation between family members, rather than de novo evolution of affiliation between family members.

The decision to cooperate is often thought to be predicated on individual assessment of environmental conditions, yet recent studies on dispersal suggest that the reality is more complicated (Clobert et al. 2012). Dispersal propensity is often tied to personality trait variation in vertebrates, which can be determined early in development and thus change the likelihood of individuals expressing a particular strategy (Cote et al. 2010, Duckworth et al. 2018). The neuroendocrine mechanisms of dispersal are poorly known for vertebrates, but repeated associations between dispersal and certain behavioral phenotypes, such as sociality and aggression (see Duckworth et al. 2018 for a review), may indicate that dispersal decisions also rest on differential regulation of the social behavior network. It is unclear whether dispersal propensity reflects an innate desire to disperse or emerges from preexisting personality variation, such as in boldness or exploratory behavior. An example of the latter case is when more aggressive individuals disperse farther, not because they want to, but because kin interactions force them to (Aguillon and Duckworth 2015). However, it is possible that shifts in composition of personalities within a population, either on ecological or evolutionary timescales (e.g., due to an increase in affiliative behavior) may enable a concomitant decrease in dispersal in response to habitat saturation.

Alternatively, evolution of philopatry may precede the formation of cooperatively breeding groups, such as when it evolves on islands (e.g., Komdeur 1992). In this scenario, an initially dispersive species colonizes an island and is constrained to philopatry, producing a forced association of family members that enables subsequent evolution of the other components of cooperative phenotypes. Indeed, Cockburn (2003) found that it was rare for cooperative species to colonize islands due to their limited dispersal, such that cooperative breeding in island endemics likely evolved secondarily. Such a secondary change may initially be induced in adults, but over time, as group interactions become more important, may lead to changes in behaviors that are mechanistically associated with others in the brain. Thus, evolution of cooperation on islands may be a particularly clear example of genetic accommodation, where an initially emergent behavior induced in adults has, over time, evolved in both form and regulation such that this strategy is expressed more frequently. In the following section, we discuss this idea further and review the evidence that the “links” between cooperative breeding behaviors may become developmentally and evolutionarily linked over time.

DEVELOPMENTAL AND EVOLUTIONARY LINKS BETWEEN COOPERATIVE BREEDING BEHAVIORS

Initially inducible traits that emerge in adulthood from a novel coexpression of preexisting variation are expected to become linked developmentally if selection favors the

obligate production of that trait (West-Eberhard 2003). At the same time, facultative expression is expected if it is adaptive for a trait to maintain environmental sensitivity (West-Eberhard 2003). While evolution of facultative cooperative strategies is similar to evolution of obligate cooperative breeding in that it is the result of adaptive evolution, it is difficult to distinguish the former from the initial emergent stage in which the trait is inducible, but not necessarily adaptive (Table 1). For this reason, it is critical to understand when the links between trait components develop.

For adaptive strategies, we expect greater sensitivity to environmental cues earlier in development than would occur for an emergent trait. In particular, personality traits are often associated with variation in social behavior, and expression of these traits is likely determined early in ontogeny well before the decision to become a helper is made. Personality traits may influence both the information gathering process as well as the costs and benefits of helping, making some individuals predisposed to help regardless of cues about constraints on independent breeding, e.g., low resource availability. Thus, here we review the evidence across species for early developmental influences on the components of cooperative breeding.

Developmental Links can Channel Organizational Shifts in Cooperative Behaviors

Most brain development occurs prenatally (Kolb 1995), although in birds, there is also a period of neuroendocrine growth and reorganization after hatching, particularly in altricial species (Charvet and Striedter 2011). Recent work demonstrates that variation in prenatal conditions can have a long-lasting influence on brain development including on structures of the social behavior network, nonapeptide, and other parts of the endocrine system that later influence behavioral expression (see Henriksen et al. 2011, Chaby 2016 for reviews). Cells producing mesotocin and vasotocin develop prenatally, and adult sex differences in nonapeptide levels and receptor expression can be influenced by prenatal exposure to sex steroids (e.g., Hammock 2015), variation in exposure to nonapeptides (e.g., Bales and Carter 2003), and prenatal stress. Prenatal administration of mesotocin decreased anxiety and increased pair-bonding behavior in adult voles (Bales and Carter 2003), while blocking mesotocin during development decreased helping and affiliative behaviors and increased aggression (see Miller and Caldwell 2015 for a review). Developmental oxytocin exposure has been shown to affect core nodes of the social behavior network in mammals, including the ventromedial hypothalamus, preoptic area, bed nucleus of the stria terminalis, lateral septum, and paraventricular nucleus, and amygdala (Gimpl and Fahrenholz 2001). Moreover, both prenatal

and juvenile stressors alter nonapeptide production in later life (Bales and Perkeybile 2012, Veenema 2012, de Souza et al. 2013).

Critically, such developmental shifts in neuroendocrine structure and function alter behavior in adulthood, often in similar directions across taxa (Potticary and Duckworth 2020). There is a wealth of evidence indicating that early-life stressors can alter HPA axis development and impact a wide range of phenotypic traits, including social behavior, aggression, dispersal, and parental care (Liu et al. 1997, Meaney and Szyf 2005, Duckworth et al. 2018, Potticary and Duckworth 2020). For example, research in Western Bluebirds (*Sialia mexicana*) provides strong evidence that these early-life stressors may influence the expression of multiple behaviors in adulthood, including the likelihood that a bird will become a helper (Potticary and Duckworth 2020). Female Western Bluebirds with higher corticosterone levels during oogenesis produced offspring that are more dispersive, aggressive, and are poor fathers, whereas females with lower corticosterone levels during oogenesis produced nonaggressive sons that are more likely to stay in the natal population, are superior fathers, and are more likely to show cooperative breeding behavior (Potticary and Duckworth 2018). Female corticosterone levels were elevated in response to multiple distinct environmental challenges; yet, the type of environmental stressor did not matter as all produced similar behavioral responses in offspring (Potticary and Duckworth 2020). This indicates that nonspecific cues of maternal stress (i.e. activation of HPA axis activity due to a variety of challenges; MacDougall-Shackleton et al. 2019) that are transmitted to offspring during development can produce correlations between behaviors associated with cooperative breeding—dispersal likelihood, social behavior, and parental care—that influence the likelihood that a young male Western Bluebird will show cooperative breeding behavior (Potticary and Duckworth 2018). Similar patterns have been found in other species. For example, prenatally stressed quail were less exploratory, more anxious, and showed increased grouping behavior (Guibert et al. 2013), a behavioral correlation commonly observed in birds (Henriksen et al. 2011). Increasing stress of rat mothers led them to produce male offspring with fewer oxytocin neurons and vasotocin neurons in the paraventricular nucleus, and these males demonstrated more anxiety-like behavior and higher aggressiveness (de Souza et al. 2013). The prevalence, consistency, and persistence of the effects of prenatal stress on later social behavior (e.g., Guibert et al. 2013, Spencer 2017) may indicate that developmental stress is a common mechanism by which population shifts in social behavior can occur. Thus, it is apparent that developmental changes of any one component of cooperative breeding depend

on and may influence other components (Bales and Perkeybile 2012, Kelly and Vitousek 2017), and can enable correlated shifts in behavior, providing support for the genetic accommodation hypothesis.

There is evidence that both prenatal and early postnatal experience of social and environmental conditions can influence neuroendocrine development to produce effects on later social and parental care behavior (Champagne and Curley 2009, Veenema 2012, Duckworth 2015, Rubenstein et al. 2016). In cooperatively breeding starlings, the amount of rainfall mothers experienced led to epigenetic changes in glucocorticoid gene expression in their sons which in turn, affected whether sons successfully bred (Rubenstein et al. 2016). In cooperatively breeding Western Bluebirds, females that lived adjacent to kin, had multiple breeding resources, and did not experience inclement weather were more likely to produce nonaggressive sons that cooperated with family members, and occasionally became helpers (Potticary and Duckworth 2018, 2020). In mammals, early-life social deprivation alters nonapeptide receptors across the social behavior network, often leading to increased anxiety and aggression, while social enrichment can produce increases in social and parental care behavior (see Veenema 2012 for a review; Champagne and Curley 2009). Social rearing environment can influence the expression of alloparental care in mammals, such that variation in family structure and individual experiences can alter bonding behaviors in adulthood, through impacts on nonapeptide receptor distributions (Ahern and Young 2009). Similarly, alloparental care in a cichlid fish was primarily determined by social interactions during development, resulting in highly repeatable cooperative phenotypes with very low heritability (Kasper et al. 2017) that differ in brain expression profiles (Kasper et al. 2018). Such environmental modulation of social development may explain how large differences in social and cooperative behaviors across cichlid taxa may arise despite high conservation of the genes underlying target nonapeptides (O'Connor et al. 2015). Given this evidence of conservation of neuroendocrine structures producing such behaviors across vertebrate taxa, it is likely that such patterns occur in avian species as well. However, the role of social environment on the neuroendocrine development of helpers in birds is not well known. Overall, these findings suggest that neuroendocrine development is responsive to both social and environmental conditions and can result in similar shifts in social behavior across disparate taxa. Importantly, such widespread developmental effects on social behaviors may explain how cooperative breeding behavior emerges, thus providing the variation upon which selection could act.

Evolutionary Outcomes of Developmental Linkages

The expression of cooperative breeding depends on individual responses to the environment, such that populations often show varying numbers of cooperative groups across space and time (Rabenold 1990, Valencia et al. 2003). Indeed, translocating bird eggs from noncooperative populations to cooperative ones can produce cooperative offspring (Baglione et al. 2002). Recent work highlights that cooperative breeding often appears in spatiotemporally variable habitats (Rubenstein and Lovette 2007, Jetz and Rubenstein 2011), and an ancestral state reconstruction indicates that cooperative species are more likely to invade harsher environments (Cornwallis et al. 2017). However, a developmental perspective provides an alternative explanation for a correlation between harsh environments and cooperative breeding. Invasion of novel, harsh habitats may perturb existing neuroendocrine systems and, given the reciprocal feedbacks between the HPA axis and the social behavior network, lead to the emergence of cooperative breeding, similar to how it can appear quickly when noncooperative species enter captivity (Skutch 1987). Under this view, the causal direction is the opposite: rather than cooperative species being more likely to invade harsher environments, noncooperative species that encounter harsh environments may be more likely to evolve cooperative behavior.

Theory suggests that a greater degree of independence between behavioral traits is expected in spatiotemporally variable habitats to allow for the flexible production of different types of behavioral repertoires (Kashtan and Alon 2005, Kashtan et al. 2007). Evolution of such modularity in birds that inhabit variable habitats may explain why they often evolve multiple facultative breeding strategies that are responsive to current environmental context. However, environmental variability can only be defined as it pertains to a species' life history, as longer-lived species are expected to experience a greater diversity of ecological contexts and problems than are short-lived species (de Lorenzana and Ward 1987). It remains an intriguing question whether populations that endure frequent environmental perturbations have more flexible behavioral repertoires. However, there is some evidence for this idea, as there is an association between cooperative breeding, longevity (Hatchwell 2009), and environmental variability (Rubenstein and Lovette 2007, Jetz and Rubenstein 2011). Thus, it is possible that cooperative breeding may be more likely to appear in variable habitats and is subsequently refined by selection if the inducing context is frequent enough. Relating the frequency that cooperative breeding is expressed within species to the degree of environmental variability may provide insight both into genetic accommodation as a process and whether species in variable environments have more flexible behavioral repertoires.

Social and environmental stress has been shown to increase affiliative behavior in social species (see [Spencer 2017](#) for a review). As shifts in affiliative behavior involve mechanisms that influence parental care behavior, it is possible that changes to affiliation mechanisms also increase the likelihood and opportunity for helping behavior to appear. That is, changes in the regulation of affiliation, in response to many social and ecological conditions, may promote changes in the neuroendocrine systems known to be involved in the regulation of aggression, group formation, and parental care behavior in other contexts. For example, open habitats have higher visibility than complex ones. Intraspecific aggression is predicted to be lower in complex environments, as the effort required to detect and expel intruders is higher (e.g., [Eason and Stamps 1992](#), [Basquill and Grant 1998](#)). Indeed, more socially and structurally complex environments produce a long-lasting influence on the development of nonapeptide systems in voles ([Prounis et al. 2018](#)). Alternatively, predation pressure may favor greater group formation in open habitats if it increases predator detection ([Duplessis et al. 1995](#)). These data suggest that reciprocal connectivity among nodes of the social behavior network, in conjunction with established feedbacks between nonapeptides and sex steroid hormones, may be able to produce similar patterns in behavioral expression. If this is the case, a shift in one aspect of the system may rapidly produce novel grouping, affiliative, or helping behavior, without selection for helping behavior per se, thus promoting the emergence of cooperative breeding.

CONCLUSIONS AND FUTURE DIRECTIONS

Cooperative breeding behavior has arisen independently across a great diversity of avian taxa ([Cockburn 2006](#)), yet when it appears, it is comprised of similar dispersal, social, and parental care behaviors. This supports the conclusion that the evolution of cooperative breeding across birds involves the emergence of cooperative breeding from novel associations of preexisting behaviors that are common to birds. Contrary to the predictions of the traditional hypothesis, the neuroendocrine mechanisms that produce these behaviors are often linked, such that similar patterns of variation in neuropeptide circuitry and social behavior network structure can produce similar behavioral phenotypes across vertebrates. Neuroendocrine associations between these conserved pathways may enable the recurrent appearance of cooperative breeding behavior and provides a resolution for how cooperative breeding can exist both as an emergent property and also as a finely tuned strategy. Specifically, the studies we review here are consistent with the genetic accommodation hypothesis in that they suggest that cooperative breeding is initially an emergent property arising from preexisting behaviors, and what evolves

is a change in the form and regulation of these behaviors to produce greater either developmental entrenchment or greater environmental sensitivity.

Our review of the neuroendocrine linkages between the underlying components of cooperative behavior points to several key directions for future work. First and foremost, we suggest that insight into the origin of cooperative breeding strategies requires a deeper understanding of neuroendocrine development within and across avian taxa. Such studies can help us to understand how dissociable the components of cooperative breeding are during development, informing both an understanding of the facultative expression of cooperative breeding within species and the evolutionary trajectories by which cooperative breeding strategies have formed. Moreover, given the recurrent appearance of cooperative breeding across species, understanding the timing and pattern of development of correlations between the behaviors comprising cooperative breeding would provide insight into whether cooperative breeding appears due to similar changes in the underlying neuroendocrine mechanisms across avian species, or if there are many neuroendocrine routes that result in cooperative breeding. Is there evidence that obligate species show earlier developmental integration of these behaviors relative to species where it is more facultative? Future research may be able to directly answer these questions by identifying the neuroendocrine mechanisms associated with cooperative breeding behavior within species and determining the developmental timing of these differences. For example, future studies may address these questions by explicitly comparing when variation in nonapeptide receptors associated with social behaviors develop in social vs. nonsocial species, or in facultative vs. obligate cooperative breeders. Moreover, activational and organizational neuroendocrine mechanisms associated with cooperative breeding, and the linkages between them, could be identified by leveraging tools such as magnetic resonance imaging (MRI) or positron emission tomography (PET) to measure the effects of hormones and nonapeptides on brain structure and function both during development and in adults. Once the mechanisms are identified, these data could be supplemented by investigating differences in expression of hormones across development in individuals or species showing cooperative behavior vs. those that do not. Experimental approaches may also uncover behavioral linkages. Selection experiments for a single behavior could be used to determine whether selection leads to concomitant changes in other behaviors, developmental changes, or correlated shifts in neuroendocrine mechanisms. Alternatively, a single type of receptor in the brain could be blocked to determine which behaviors are influenced. The durability and developmental timing of such linkages may also be investigated using cross-fostering experiments; for example, by manipulating maternal stress and then

cross-fostering offspring to determine whether this produces an effect on the brains and behavior of offspring.

This review furnishes new questions for the evolution of different types of cooperative groups. For instance, are the neuroendocrine mechanisms underlying kin-based cooperative groups the same as those for non-kin groups? Evolutionarily, what types of affiliative behavior are more likely to enable the appearance of cooperative breeding—increased flocking behavior, or affiliative behavior in other contexts, such as group foraging or dispersal? Does cooperative breeding evolve in a sequential fashion, requiring the evolution of increased affiliation or limited dispersal prior to the emergence of cooperative breeding? Comparative studies that explicitly map variation in the ontogeny and expression of the social behavior network across cooperative and noncooperative species could also be used to provide inference into the process by which cooperative breeding evolves relative to other social behaviors.

There is already a vast amount of information on the neuroendocrine basis of social behavior across a diversity of vertebrate taxa, some of which we have summarized here. All that is needed now is to apply what is known about regulation of social behavior in vertebrates in general to avian taxa that span the spectrum from species that never show cooperative breeding to facultative and obligate species. Such studies may provide insight into both the longstanding and unresolved questions about the evolution of cooperative breeding, as well as the evolution of complex behavior across taxa more broadly.

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