Physiology & Behavior xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/physbeh

The *neoteny-helper hypothesis*: When to expect and when not to expect endocrine mechanisms to regulate allo-parental care?

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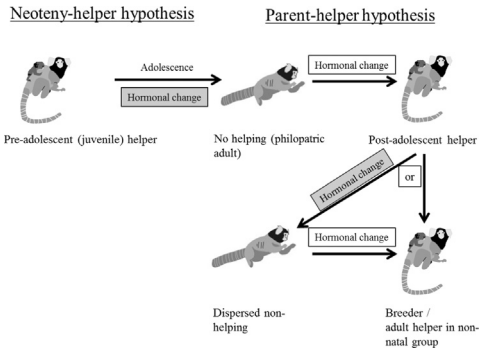
GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Reproductive suppression
Puberty
Adolescence
Cooperative breeding
Helping
Sexual maturity

ABSTRACT

Family groups with helpers occur in several species of fish, birds and mammals. In such cooperatively breeding species all group members help with raising the offspring, i.e. parents and offspring from previous litters. While the ecological reasons and ultimate consequences of allo-parental care have been studied in detail, we know little about its physiological regulation. We propose three alternative hypotheses for the endocrine regulation of allo-parental care. 1. The *neoteny-helper hypothesis* predicts that helpers that did not undergo adolescence yet show helping behavior without any endocrine mechanisms activating it, as helping is the default response towards infant stimuli. The endocrine changes during adolescence would then deactivate helping behavior. 2. The *parent-helper hypothesis* predicts that helpers undergo the same endocrine changes as parents (increased prolactin and corticosterone levels; decreased testosterone in males but increased estrogen in females). We predict that this hypothesis is especially important in post-adolescent helpers. 3. The *helper-specific hypothesis* predicts that there are specific endocrine mechanisms that only exist in helpers but not in breeders. We review evidence for these three hypotheses in 23 species of fish, birds, and mammals. We found no evidence for the *helper-specific hypothesis* but for both other hypotheses. As predicted, this depended on whether helpers were pre- or post-adolescent, but information on whether or not helpers underwent adolescence was often missing. Thus, future studies should investigate whether or not helpers have reached sexual maturity, differentiate between pre- and post-adolescent helpers, and study behavioral changes in helping behavior during adolescence. We conclude that the neurobiological circuits in the brain necessary for allo-parental care might often be the default stage in

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https://doi.org/10.1016/j.physbeh.2017.12.008
Received 30 June 2017; Received in revised form 6 December 2017; Accepted 6 December 2017

helpers from cooperative breeding species, which might be deactivated by specific endocrine mechanisms during adolescence, and then would need reactivation for allo-parental and parental care.

1. Introduction

Many animal groups form because of the delayed dispersal of adult offspring, such that family groups develop [1]. In such family groups, cooperative breeding might occur, i.e. individuals help to rear offspring that are not their own [2]. Helping behavior includes territory defense, defense of nest and young against predators, nest building, babysitting, feeding, warming and cleaning of the young [2,3]. It can improve the development [4] and survival of offspring [5–8], or increase the rate at which offspring are produced [9] (but see also [10,11] for no effect of the presence of helpers). Cooperative breeding has been extensively studied in several mammal, bird and fish species, including field experiments to test for the ultimate reasons of philopatry and helping by non-breeders [12–15].

Over the last decades, most research on cooperative breeding focused on its evolutionary causes. By contrast, comparisons of underpinning physiological mechanisms between breeders and helpers remain rare. For example, increased prolactin levels during the period of chick rearing have been reported in breeders and helpers of Harris hawks, red-cockaded woodpeckers and Florida scrub jays [16–18]. Testosterone levels are similar between male breeders and helpers in red-cockaded woodpeckers [16], azure-winged magpies [19] and the cichlid fish *Neolamprologus pulcher*[20]. In contrast, helpers have lower testosterone levels in scrub-jays of the genus *Aphelocoma*[18,21], white-browed sparrow weavers [22] and superb fairy-wrens [23]. Male meerkats that are willing to feed pups have increased cortisol levels and a moderate increase in prolactin, while testosterone levels are not associated with helping behavior in this species [24]. Even fewer studies exist that took female helpers into account. In Florida scrub-jays, female helpers have lower estradiol and corticosterone levels than female breeders [21], and in common eiders helping females have elevated prolactin levels comparable to those of mothers [25]. In sum, while field studies on the neuro-endocrinology of helping behavior are emerging, a conceptual framework is missing that could explain the species-specific and often variable endocrine patterns.

Here, we present three different hypotheses regarding how helping behavior might be regulated in non-breeders and review the existing literature to examine in how far it supports each hypothesis: 1. The *neoteny-helper hypothesis*, 2. the *parent-helper hypothesis*, and 3. the *helper-specific hypothesis*. By proposing alternative hypotheses we hope to improve the formulation of predictions for future empirical studies on the neuro-endocrinology of helping behavior by non-breeders (and to some extent also allo-parental care by breeders).

First, we propose the novel *neoteny-helper hypothesis* predicting that helping could be the basic behavioral pattern present in helpers which did not yet undergo adolescence. Adolescence, also called puberty, refers to the process of sexual maturation and as such the gradual transition from juvenile individuals to sexually mature adults [26–28]. For instance, in California mice (*Peromyscus californicus*) and laboratory rats, juveniles of both sexes show allo-parental care without evidence of endocrine changes [29,30]. In contrast, adult non-parents kill strange pups and endocrine mechanisms are involved to activate parental care once adults become parents. Hence, delayed onset of adolescence in philopatric offspring (often due to sexual suppression [31–33]) could be a mechanism to maintain females and males in the juvenile endocrine state, in which they are ready to show alloparental care. The *neoteny-helper hypothesis* therefore predicts that helpers which do not undergo adolescence show no endocrine changes related to helping behavior.

Second, the traditional *parent-helper hypothesis* proposes that the physiological mechanisms of helping behavior are the same as of parental care. Parental males and females typically have increased prolactin levels [34] and decreased testosterone levels, especially in males [35,36] (though some testosterone is needed to activate normal behavior including parental care [37,38]), whereas female mammals show increased estrogen and progesterone levels during pregnancy that activate maternal behavior [39]. Some of the endocrine responses are sex-specific, for example glucocorticoids, which are often increased in mothers but can be decreased in fathers showing parental care [40]. The *parent-helper hypothesis* predicts that the same endocrine patterns observed in parents expressing parental care should also be observed in non-breeding helpers.

Third, there might be endocrine mechanisms that evolved specifically to regulate helping behavior in non-breeders, which differ from the mechanisms regulating parental care. We refer to this as the *helper-specific hypothesis.* It predicts that endocrine changes are observed in helpers, but that these changes differ from those observed in breeders.

It is important to note that the three physiological pathways mentioned above are not mutually exclusive. The mechanisms involved in the *neoteny-helper hypothesis* might work in individuals that by age and body mass could be regarded as adults but are not sexually mature and in juveniles, whereas in post-adolescent helpers the same endocrine mechanisms as in parents might occur, representing the *parent-helper hypothesis*. In our current review, we present an overview of the results from studies on fish, birds, and mammals where hormone levels were measured in both non-breeding helpers and in parents. Our aim was to review empirical evidence of the three proposed mechanisms, to enable better hypothesis testing for future empirical studies. Specifically, we determined in how far the endocrine patterns described in non-breeding helpers fit with the predictions associated with each of the three different hypotheses (Table 1).

2. Literature survey

We searched specific journals known to publish research in the field of behavioral endocrinology using four specific keywords: 1. alloparental care, 2. allo-parental care, 3. helper, and 4. cooperative breeding. Every paper was then checked for information on the endocrine status of helpers, as well as for corresponding information on breeders. For each taxa, we conducted a literature research in the following five journals: *Animal Behaviour*, *General and Comparative Endocrinology*, *Hormones and Behavior*, *Journal of Comparative Physiology B* and *Physiology and Behavior*. We additionally searched for publications in

Table 1
Predictions of how the levels of four specific hormones should differ between helpers and breeders depending on the *neoteny-helper*, the *parent-helper* and the *helper-specific hypotheses*.

	Prolactin	Glucocorticoids	Testosterone (males only)	Estrogen (females only)
Neoteny-helper hypothesis	< (no change)	< (no change)	No change in helpers but decrease in breeders	< (no change)
Parent-helper hypothesis	=(increase)	= (increase in females)	= (decrease)	=(increase)
Helper-specific hypothesis	< or >	< or >	< or >	< or >

> / < / =: Helpers are expected to have higher/lower/similar hormone levels compared to breeders.