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The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*

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ABSTRACT

The conundrum of why subordinate individuals assist dominants at the expense of their own direct reproduction has received much theoretical and empirical attention over the last 50 years. During this time, birds and mammals have taken centre stage as model vertebrate systems for exploring why helpers help. However, fish have great potential for enhancing our understanding of the generality and adaptiveness of helping behaviour because of the ease with which they can be experimentally manipulated under controlled laboratory and field conditions. In particular, the freshwater African cichlid, *Neolamprologus pulcher,* has emerged as a promising model species for investigating the evolution of cooperative breeding, with 64 papers published on this species over the past 27 years. Here we clarify current knowledge pertaining to the costs and benefits of helping in *N. pulcher* by critically assessing the existing empirical evidence. We then provide a comprehensive examination of the evidence pertaining to four key hypotheses for why helpers might help: (1) kin selection; (2) pay-to-stay; (3) signals of prestige; and (4) group augmentation. For each hypothesis, we outline the underlying theory, address the appropriateness of *N. pulcher* as a model species and describe the key predictions and associated empirical tests. For *N. pulcher*, we demonstrate that the kin selection and group augmentation hypotheses have received partial support. One of the key predictions of the pay-to-stay hypothesis has failed to receive any support despite numerous laboratory and field studies; thus as it stands, the evidence for this hypothesis is weak. There have been no empirical investigations addressing the key predictions of the signals of prestige hypothesis. By outlining the key predictions of the various hypotheses, and highlighting how many of these remain to be tested explicitly, our review can be regarded as a roadmap in which potential paths for future empirical research into the evolution of cooperative breeding are proposed. Overall, we clarify what is currently known about cooperative breeding in *N. pulcher*, address discrepancies among studies, caution against incorrect inferences that have been drawn over the years and suggest promising avenues for future research in fishes and other taxonomic groups.

Key words: cooperative breeding, *Neolamprologus pulcher*, altruism, helping, alloparental care, kin selection, pay to stay, signals of prestige, group augmentation.

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I. INTRODUCTION

In cooperatively breeding species, subordinate individuals typically forego their own reproductive efforts and help to raise the offspring of dominant breeders. Understanding the evolution of this behaviour has proven to be an enduring research challenge for evolutionary biologists (Hamilton, 1964*a*,*b*; Brown, 1987; Emlen, 1991; Russell, 2004; Clutton-Brock, 2002, 2009). Attempts to address the evolution of helping usually break the problem down into three questions (Brown, 1987): (1) why do subordinates stay rather than disperse to breed independently elsewhere; (2) why do subordinates forego breeding within the group; and (3) why do subordinates help rear the offspring of breeders? The first question of why non-breeding subordinates should stay focuses on identifying the benefits and constraints that promote delayed dispersal and hence group formation. The majority of such investigations have been conducted on birds, mammals and social insects, with much debate continuing to surround the relative importance of life history *versus* ecology, as well as the type of ecological factors promoting delayed dispersal in such taxa (Arnold & Owens, 1998; Field *et al.*, 1998; Hatchwell & Komdeur, 2000; Cockburn, 2003; Russell, 2004; Dickinson & Hatchwell, 2004). Similarly, the second question of why subordinates might forego breeding and the general issue of reproductive skew within social groups remains a source of considerable contention, with empirical investigations generating equivocal results and once again being limited to birds, mammals and social insects (Reeve & Keller, 2001; Magrath, Johnstone & Heinsohn, 2004; Hager & Jones, 2009).

The third question of why non-breeders should help dominant breeders presents a significant evolutionary challenge. This is because helping is costly to helpers owing to missed reproductive opportunities elsewhere (Brown, 1987) and the act of helping itself (Russell *et al.*, 2003), while the recipients of help benefit in the form of enhanced reproductive output (Emlen, 1991; Dickinson & Hatchwell, 2004; Russell, 2004). This problem of apparent altruism has inspired a number of theoretical ideas that explain the factors compensating for such costs and thus why such cooperative breeding could have evolved and be maintained in many species (Hamilton, 1964*a*,*b*; Gaston, 1978; Emlen & Wrege, 1989; Zahavi, 1995; Pen & Weissing, 2000; Kokko, Johnstone & Clutton-Brock, 2001; Kokko, Johnstone & Wright, 2002). Once again, the primary model species used to address these theoretical developments have been birds, mammals and social insects (Solomon & French, 1997; Koenig & Dickinson, 2004; Cockburn, 1998; Bourke & Franks, 1995; Queller & Strassman, 1998; Field & Foster, 1999).

While the questions of why to delay dispersal, why to forego breeding and why to help have received relatively little attention in fish, fish actually offer an ideal opportunity to study all three owing to the ease with which their social and reproductive systems can be experimentally manipulated under controlled laboratory and field conditions, and because individuals can be uniquely tagged enabling continued observations of the same individuals and groups over time. The first fish species described to exhibit cooperative

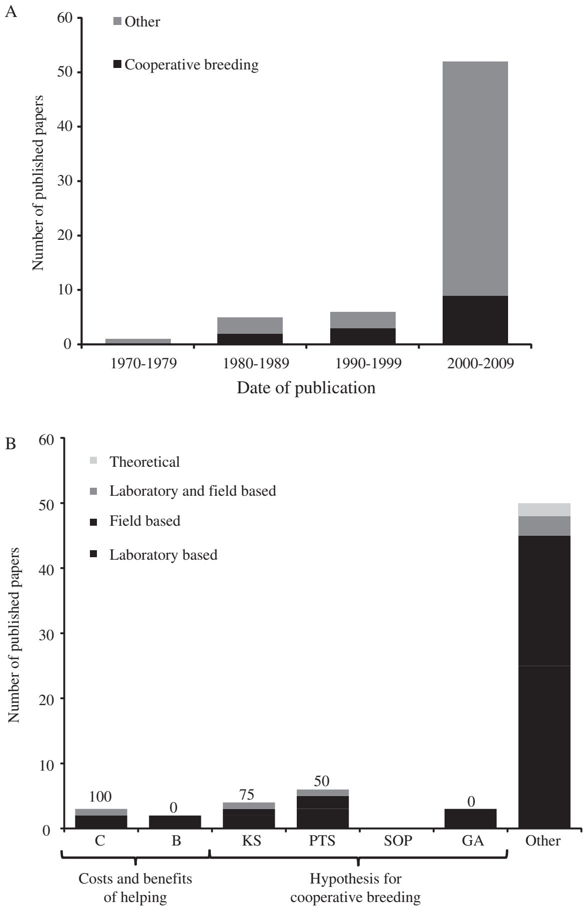

Fig. 1. (A). Total number of publications on the social and reproductive behaviour of *N. pulcher* from 1970 to 2009, split according to research relating to cooperative breeding (black bars) *versus* other social or reproductive behaviours (grey bars). 'Other' papers have primarily assessed dispersal behaviour, mating systems, dominance interactions, conflict over rank, reproductive parasitism, group-living decisions and hormonal correlates of behaviour. (B) Number of publications in relation to the subject or hypothesis addressed. C = costs to helpers, B = benefits to breeders, KS = kin selection, PTS = pay-to-stay, SOP = signals of prestige, GA = group augmentation. All published papers are split according to whether the study was conducted in the laboratory (black), field (dark grey), both laboratory and field (medium grey), or are theoretical (light grey). Numbers above the bars represent the percentage of total studies that addressed a key prediction of the hypothesis.

breeding behaviour, the freshwater African cichlid, *Neolamprologus pulcher*, still remains the best studied (Coeckelberghs, 1975; Taborsky & Limberger, 1981). Since its discovery, *N. pulcher* has emerged as a promising model organism for investigating why helpers help. Over the past three decades, this species has been the subject of intense empirical investigation, with 64 papers published to date (Fig. 1A). The last decade, in particular, has seen an explosion of research on this species. Interestingly, the majority of this research has focused on other aspects of social and reproductive characteristics besides those relating to cooperative breeding (Fig. 1A). Even so, the evolution of cooperative breeding in *N. pulcher* has proven to be an enduring area of research, with a total of 15 published papers directly addressing this topic so far. Of the four key hypotheses proposed to explain why helpers help, the pay-to-stay model (Gaston, 1978) has received the most empirical attention, followed by kin selection (Hamilton, 1964*a*,*b*) and group augmentation (Woolfenden, 1975; Kokko *et al.*, 2001), and finally the signals of prestige hypothesis (Zahavi, 1995) which has yet to receive any empirical attention in *N. pulcher* (Fig. 1B). Research has been relatively evenly spread between studies conducted in the field and those conducted in the laboratory (Fig. 1B).

In this review, we focus specifically on addressing why helpers help by critically assessing our current understanding of the costs and benefits of helping in *Neolamprologus pulcher*. We examine four hypotheses for why help has evolved: (1) kin selection; (2) pay-to-stay; (3) signals of prestige; and (4) group augmentation. We distill each hypothesis down to its key predictions, and then review the empirical evidence for *N. pulcher* pertaining to each hypothesis. In so doing, we aim to illustrate the extent to which each hypothesis can be accepted as an explanation for helping, and highlight and reconcile inconsistencies or contradictory support for any given hypothesis that may exist. Finally, we discuss future directions of empirical and theoretical research that should be incorporated into the next wave of studies as a means of fully elucidating the adaptive significance of helping in this and other species in general. Overall, we aim to promote the cross-fostering of research ideas by highlighting the recent developments in *N. pulcher* research for those using model cooperatively breeding systems from other taxa, whilst illustrating the bench marks set by studies from these other taxa for those using *N. pulcher* or other fish model systems.

II. STUDY SPECIES

Social groups of *Neolamprologus pulcher* can be found on rocky substrata in the southern basin of Lake Tanganyika in waters 3–45 m deep (Taborsky & Limberger, 1981; Balshine-Earn *et al.*, 1998). Groups of these fish co-defend a small territory (mean area = 0.315 m^2, range 0.775–1.01 m^2) made up of rocks or crevices in boulders (Balshine *et al.*, 2001, Fig. 2). These rocks and crevices are used as both shelters and breeding substrata. Social groups are found clustered into colonies or sub-populations of two to >100 groups (Taborsky, 1984; Stiver *et al.*, 2004, 2007; Fig. 3); the average distance between two social groups within such colonies is 1.6 m and the average distance between two colonies is 22.3 m (Stiver *et al.*, 2007; Fig. 3).

A social group of *N. pulcher* is made up of a dominant breeding pair and 0–20 smaller subordinates called helpers (Taborsky, 1984, 1985; Balshine *et al.*, 2001; Heg *et al.*, 2005; Desjardins *et al.*, 2008*a*; Fig. 4). The reported average group size ranges from approximately seven (Balshine *et al.*, 2001) to nine (Heg *et al.*, 2005) individuals. In each social group the

Fig. 2. *Neolamprologus pulcher* against its typical rocky habitat substratum. The mean ± S.D. body size (cm standard length) for breeder males is 6.0 cm ± 0.3 cm (N = 60), for breeder females is 5.2 cm ± 0.3 cm (N = 89), and for helpers is 3.6 cm ± 1.3 cm (N = 178) (Balshine *et al.*, 2001). Photo credit: Julie Desjardins.

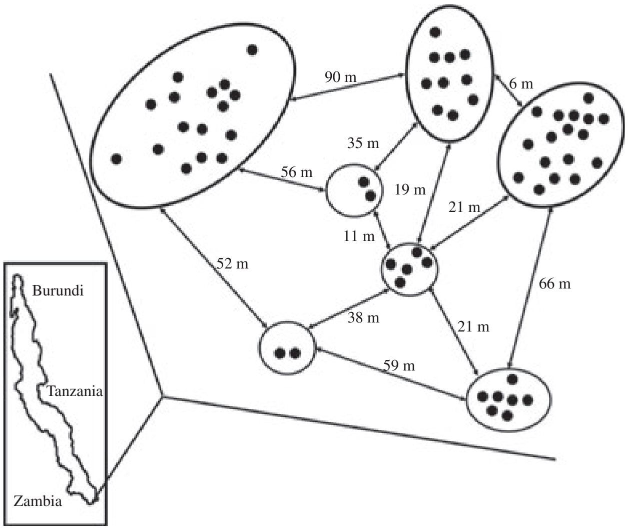

Fig. 3. A graphical representation of the territories and subpopulations of *Neolamprologus pulcher* at Kasakalawa Bay at the Southern tip of Lake Tanganyika, Zambia. Note that territories (dots) are clustered into subpopulations (open circles). Sizes and distances are not drawn to scale. On average the mean distance between two adjacent territories is 1.6 m and the mean distance between subpopulations is 22.3 m. Taken from Stiver *et al.* (2007).

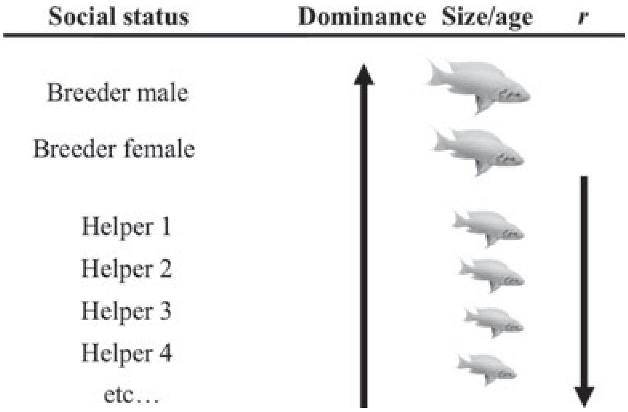

Fig. 4. The social structure of *Neolamprologus pulcher* groups. Breeder males are the largest group members, typically followed by breeder females and helpers. Helpers are organized into a size-based dominance hierarchy, where helper $\mathcal{N}$ is dominant over helper $\mathcal{N}+1$. Smaller helpers are more closely related to dominant breeders than are larger helpers related to dominant breeders (r = relatedness to dominants).

breeding male is always the largest individual (5.6–7.0 cm in standard length), the breeding female is usually the next largest fish in the social group (4.8–6.0 cm) while subordinate helpers are generally smaller (1.5–6.4 cm; Fig. 4). Helpers are organised into size-based dominance hierarchies within groups, which reflect two queues for breeding status—one for males and the other for females (Balshine-Earn *et al.*, 1998; Werner *et al.*, 2003; Heg, Bender & Hamilton, 2004*b*; Hamilton, Heg & Bender, 2005; Fitzpatrick *et al.*, 2008). Although group dynamics are reasonably stable over time, fish will either inherit the dominant breeding position from within their social group or leave their social group (disperse) either to take over a dominant breeding position in another group or to become a more dominant helper in another group (Stiver *et al.*, 2004; Fig. 5). Females more commonly take the inheritance route to reproduction whereas males more commonly disperse to take over new groups (Stiver *et al.*, 2004, 2006; Bergmüller *et al.*, 2005*a*; Fig. 5).

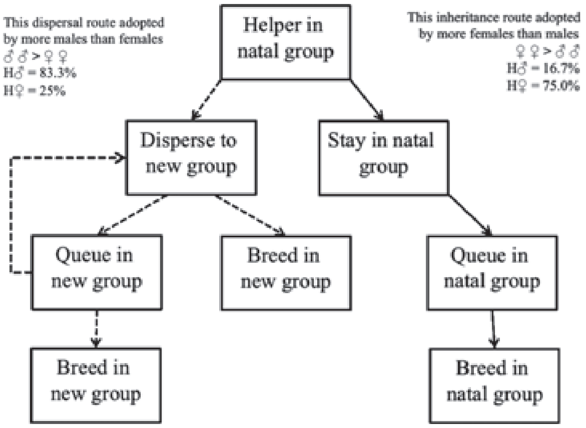

Fig. 5. Routes to reproduction for helpers in *N. pulcher*. Dashed lines represent typical routes for male helpers; solid lines represent typical routes for female helpers. The percentage of cases in which helper males and females achieved breeding status *via* each route is shown. Percentages are adapted from breeder removal experiments conducted by Stiver *et al.* (2006) under natural conditions. Reported values are the percentage of cases when considering only groups where a breeder removal event actually occurred.

Table 1. Pattern of workload among group members in relation to physical, social and reproductive factors. MG = monogamous group, PG = polygynous group, L = large, S = small, HR = high rank, LR = low rank, BC = broodcare, TD = territory defence, TM = territory maintenance, ? = not known, n/a = not applicable. Asterisks and numbers refer to studies that have specifically addressed variation in helping effort under natural conditions in relation to the factor in question: *[1] Balshine *et al.* (2001), *[2] Stiver *et al.* (2005), *[3] Desjardins *et al.* (2008*a*,*b*), *[4] Desjardins *et al.* (2005)

Factors influencing workload	Male breeders	Helpers	Female breeders
Sex	Lowest level	Intermediate level ♀ > ♂*[2]	Highest level
Size	?	L = S*[2]	?
Rank	n/a	HR = LR*[2]	n/a
Mating system	MG > PG*[3]	MG = PG*[3]	MG > PG*[3]
Type of work/help	BC > TD > TM*[4]	BC > TD > TM*[1]	BC > TD = TM*[4]

While some researchers have treated *Neolamprologus pulcher* as a monogamous species (Hirschenhauser *et al.*, 2008), the existence of large males holding haremic positions in multiple groups has been known since the first investigations of *N. pulcher's* behaviour in the field (Limberger, 1983), and polygyny confirmed in further investigations of the mating behaviour of this species (Desjardins *et al.*, 2008*a*).

Both breeders and helpers will defend the territory (against predators, conspecific neighbours and heterospecific territory competitors), maintain the territory (by digging and removing debris) and care for the brood (by cleaning and fanning eggs and defending the young) (Taborsky & Limberger, 1981). These three behaviours—territory defence, territory maintenance and brood care—are commonly combined to give an overall index of helping effort, allocare or workload. Individuals vary in the extent to which they perform these helping behaviours. Typically the breeding female is the most active and the breeding male is the least active, with helpers being of intermediate activity (Balshine *et al.*, 2001; Table 1). Female helpers do more work than male helpers (Stiver *et al.*, 2005) and breeder males and females in monogamous groups do more work than those in polygynous groups (Desjardins *et al.*, 2008*a*; Table 1).

III. DO HELPERS REALLY HELP?

Here we follow the definition of a cooperative behaviour used by Bergmüller *et al.* (2007) and Buston & Balshine (2007), as a behaviour that is initially costly for the donor (helpers) but ultimately enhances the fitness of both the donors and recipients (breeders) of the behaviour relative to if the behaviour were not expressed. We acknowledge that the use of the term 'cooperative behaviour' varies widely across fields, so we invite readers simply to substitute their own terms for the behaviour we discuss.

(1) Immediate reproduction by helpers

The most parsimonious explanation for 'helping' behaviour is that individuals are actually directly and immediately enhancing their own selfish interests by caring for their own offspring. In these cases, the behaviour of subordinates would not be classified as helping (or as being cooperative) and there would be no conundrum of why helpers help. Since direct helper reproduction has been documented in many other cooperatively breeding species (e.g. Keane *et al.*, 1994; Whittingham, Dunn & Magrath, 1997; Reeve *et al.*, 2000; Griffin *et al.*, 2003), it is important to address the possibility of immediate reproduction by 'helpers' in *N. pulcher* before addressing why helpers help. For *N. pulcher*, there is mounting genetic evidence, primarily from laboratory studies, that helpers may be engaging in direct reproduction within the group (Dierkes, Taborsky & Kohler, 1999; Heg *et al.*, 2006, 2008*b*, 2009; Dierkes, Taborsky & Achmann, 2008; Heg, 2008; Heg & Hamilton, 2008; Stiver *et al.*, 2009). Although the occurrence of helper reproduction is relatively rare, it suggests that helping behaviour could potentially be related to the ability or opportunity for direct helper reproduction. Heg *et al.* (2009) found that helper females who provided care for the dominant female's broods produced eggs themselves, leading them to suggest that helpers may in fact be helping as a payment to breed within the group. In other words, helpers help because helping entitles them to a share of immediate reproductive benefits, although alternative explanations can not be ruled out owing to the correlational nature of this study. Even so, these results are significant for two reasons. Firstly, they represent a step towards linking the occurrence of immediate reproductive benefits with the evolution of helping behaviour in *N. pulcher*. Secondly, they highlight the fact that broodcare has the potential to reflect direct parental care by helpers rather than helping, thus placing the evolutionary significance of this behaviour in a completely different light.

To determine whether immediate reproductive benefits promote 'helping', the extent to which helpers reproduce must be quantified. Thus far, there is a clear discrepancy between laboratory and field studies that needs to be addressed. For helper males, laboratory studies have found that they do contribute to fertilizations (Dierkes *et al.*, 1999; Heg *et al.*, 2008*b*) but field studies have been unable to assign any paternity to helpers (Dierkes *et al.*, 2008; Stiver *et al.*, 2009). Any extra-pair paternity can so far only be confidently assigned to other neighbouring males (Stiver *et al.*, 2009). For helper females, laboratory studies have found that they do engage in direct reproduction (Heg, 2008; Heg & Hamilton, 2008; Heg *et al.*, 2009), and in the field, female helpers have also been found to contribute to broods of the breeder female (Stiver *et al.*, 2009). Future research should aim further to clarify, using larger sample sizes under natural conditions, the relative frequency with which helpers *versus* other conspecifics from outside the group share in parentage within groups.

(2) Benefits of helping to breeders

Investigations into whether helping benefits breeders are an important step for confirming whether a behaviour can be defined as cooperative. In addition, quantification of the net benefits to breeders is important for indicating which of the alternative hypotheses are likely to promote helping, since not all hypotheses for help require helping to result in a net positive effect on breeder fitness. In other words, helping can serve simply to offset the costs of having a subordinate around, thus providing benefits to breeders relative to if the subordinate did not help, but resulting in a neutral rather than positive overall effect on breeder fitness (Kokko *et al.*, 2002; Buston & Balshine, 2007) (Table 2). In the current section, we deal with the evidence pertaining to the benefits of helping for breeders and hence whether helpers really help. Potential benefits to helpers are considered in Section V.

There is considerable evidence from both the laboratory and field to suggest that the presence of helpers is beneficial to breeders as measured by various proxies of breeder fitness (Taborsky, 1984; Balshine *et al.*, 2001; Brouwer, Heg & Taborsky, 2005; Taborsky, Skubic & Bruintjes, 2007). Using groups maintained in the laboratory, Taborsky (1984) found that absolute breeding success (a combined measure of clutch size and egg survival probability) was higher for breeding pairs with helpers compared to those without helpers. In another laboratory study, Taborsky *et al.* (2007) found that egg size was negatively correlated with the number of helpers within groups, suggesting that the presence of helpers enables breeder females strategically to reduce investment per egg in a manner which maximizes breeder fitness. Under natural field conditions, Balshine *et al.* (2001) documented a positive correlation between the number of helpers in a group and the number of fry emerging, and Brouwer *et al.* (2005) found that fry survival was lower in groups from which helpers had been experimentally removed compared to intact groups.

While these studies are consistent with helper presence being beneficial for breeders, there are four main limitations. First, since territory size is positively correlated with the number of helpers in a group (Balshine *et al.*, 2001), any positive relationship between the number of helpers and breeder fitness could in fact have been driven by territory size (Brown, 1987; Emlen, 1991). Second, helper removal experiments are sometimes considered problematic because they disrupt the social hierarchy (Cockburn, 1998). Third, effects of helper removals on breeder fitness can be masked because mothers may modify their levels of parental investment depending on the number of helpers present (known as 'maternal effects'; Russell *et al.*, 2007; Russell & Lummaa, 2009). Fourth, it is not clear exactly what aspect of a helper's presence actually confers the proposed benefits. The key issue pertaining to whether helpers really help is whether the cooperative behaviour *per se*, rather than the mere presence of helpers, is beneficial for breeders (Buston & Balshine, 2007; Balshine & Buston, 2008). Disentangling the impact of the presence of helpers from the impact of help itself could be achieved experimentally, using controlled manipulations such as that developed by Bergmüller & Taborsky (2005). In this laboratory experiment, barriers were used to manipulate the levels of help a helper could provide whilst maintaining the helper within visual contact with the rest of the group. In this case, Bergmüller & Taborsky (2005) employed their methodology to examine the short-term effects of reduced helping on subsequent social interactions rather than the long-term impacts of reduced helping on breeder reproductive success. Even so, this methodology provides a useful way forward, particularly if conducted under natural field conditions. In addition, isolating the effects of helping from helper presence could be achieved statistically, by controlling for the effects of group size (i.e. the presence of helpers) and helping effort on breeder reproductive success. If breeder reproductive success is still positively associated with helping effort after controlling for group size, this would support the fact that helping *per se* is indeed beneficial to breeders.

Table 2. Summary of the expected relationships between various factors and helping effort for each of the alternative hypotheses. **+** represents positive expected relationships, **−** represents negative expected relationships, and 0 represents no expected relationships

	Alternative hypotheses			
Predicted relationship between:	Kin selection	Pay to stay	Signals of prestige	Group augmentation
Relatedness and helping effort	$+^{\text{crit}}$	0^{*1}	0	0
Helping effort and likelihood of punishment	0	$-^{\text{crit}}$	0	0
Punishment and subsequent helping effort	0	$+^{\text{crit}}$	0	0
Need for help and punishment	0	+	0	0
Presence of audience and helping effort	0	+	+	0
Helping effort and receipt of social rewards	0	+	$+^{\text{crit}}$	0
Individual quality and helping effort	+	0	$+^{\text{crit}}$	+
Helping and net effect on breeder fitness	$+^{\text{crit}}$	0^{*2}	0	$+^{\text{crit}}$

[*1] Negative relationship predicted if helping also driven by kin selection (Kokko *et al.*, 2002).
[*2] Pay-to-stay predicts no net change in breeder fitness as helpers help only to offset costs of their presence (Kokko *et al.*, 2002).
$^{\text{crit}}$identifies critical predictions which if not upheld would lead to rejection of the hypothesis.

IV. IS HELPING COSTLY TO HELPERS?

Not only must helping provide benefits to breeders, but it must also be temporarily altruistic (imposing a net cost) on helpers in order to be considered an evolutionary puzzle. Assessments of the nature and magnitude of costs are therefore necessary to distinguish between altruistic *versus* mutualistic forms of cooperation (see Section VI.6), to understand why helping effort can vary so considerably among individuals (Heinsohn & Legge, 1999; Russell *et al.*, 2003; Heinsohn, 2004) and to quantify the long-term inclusive fitness consequences of helping for helpers (see Section VI; Table 3). Investigations into the costs of helping in *N. pulcher* were pioneered by Taborsky (1984) who assessed costs in terms of negative impacts on helper growth. In a laboratory experiment, he showed that the growth rates of helpers were lower than those of similarly sized non-helping territorial fish (territorial controls) and non-territorial fish (non-territorial controls), suggesting an energetic cost to helping. However, Taborsky (1984) pointed out that the reduced growth rates observed may not necessarily be attributed to the energetic costs associated with help, but may alternatively have arisen as a result of growth suppression due to conflict over rank within the hierarchy. This alternative growth suppression perspective is supported by the observation that helpers grew more slowly than territorial control fish, the latter of which also performed territory maintenance, defence and brood care (Taborsky, 1984). Furthermore, growth rates of the largest helpers, presumably the greatest competitive threat to breeders, were lower than the growth rates of other helpers within groups. As such, this study points more towards status-dependent growth suppression, as was later confirmed in this species (Heg *et al.*, 2004*b*; Hamilton & Heg, 2008), instead of an energetic cost to helping.

More precise physiological costs of helping were later documented by Taborsky & Grantner (1998) and Grantner & Taborsky (1998). These researchers performed a detailed series of laboratory tests in which direct measures of the metabolic expenditure resulting from territory maintenance (one form of helping), agonistic and submissive behaviours were obtained. All three behaviours resulted in significant increases in metabolic rates relative to routine and standard metabolic rates. In terms of energetic costs however, digging was not energetically more expensive than either agonistic or submissive behaviours. Using time-budget analyses, Taborsky & Grantner (1998) then showed that only a small proportion (1.5%) of the total energy expended during a breeding cycle was spent on helping and other social behaviours, the rest (98.5%) being devoted to general bodily maintenance activities such as feeding. Of the small amount of time spent on helping and social behaviours, the majority was expended on submissive behaviours, followed by agonistic behaviours, then territory maintenance and broodcare (Taborsky & Grantner, 1998). It follows that the energy expended on helping, at least in terms of territory maintenance and broodcare, amounts to less than 1.5% of the total energy expenditure of helpers per breeding cycle. Whether this is a biologically significant energetic cost, in terms of having an impact on lifetime helper fitness, has yet to be ascertained.

Table 3. Quantifying the inclusive fitness of helpers and breeders from helping. X_i and X_j are measures of direct fitness effects of helping *versus* not helping for helpers. Y_i and Y_j are measures of the direct fitness effects of receiving help *versus* not receiving help for breeders, and the indirect fitness effects of helping *versus* not helping for helpers. From the helper's perspective, if helpers gain direct benefits from helping, we expect $X_i - X_j > 0$. If helpers gain indirect benefits from helping, we expect $r(Y_i - Y_j) > 0$. From the breeder's perspective, if help is a cooperative behaviour, we expect $Y_i - Y_j > 0$

Fitness component	Description
X_i	Fitness of a helper that helps i.e. average lifetime reproductive success (e.g. no. offspring produced or surviving) of helpers that have helped*
X_j	Fitness of a helper that does not help i.e. average lifetime reproductive success of helpers that have not helped
Y_i	Fitness of breeder as a result of helping *per se* i.e. average lifetime reproductive success in a group of average size**
Y_j	Fitness of breeder without helping *per se* but in presence of helpers i.e. average lifetime reproductive success in a group of average size in which helpers are prevented from helping
r	Average coefficient of relatedness between breeders and helpers

*X_i is the sum of (i) a negative impact on fitness (given cooperative behaviours are initially altruistic) and (ii) a positive impact on fitness (because cooperative behaviours are ultimately selfish).
**Taking the average group size is necessary because breeder fitness will vary depending on the number of helpers helping.

Energetic costs of territory maintenance thus have been well documented in *N. pulcher*, although their impact on lifetime helper fitness remains unclear. In other taxa, specifically birds and mammals, costs of helping are primarily manifested as reduced mass, growth and survival of individuals, rather than long-term reproductive costs (Russell *et al.*, 2003; Heinsohn, 2004). Therefore, to obtain a more comprehensive picture of the costs of helping in *N. pulcher*, and to promote greater cross-taxonomic comparisons of the nature of such costs, future research should focus on quantifying the potential energetic, survival and long-term reproductive costs of each different form of helping behaviour (territory defence, territory maintenance and broodcare). Ideally, the amount of help provided by helpers should be experimentally manipulated (for example by forcing them to help more or less than normal) and any subsequent detrimental or beneficial impacts on helper fitness quantified. This is because helpers are likely to set levels of helping according to their ability, making it difficult to measure costs without experimentation or carefully controlled intra- or inter-individual comparisons (Heinsohn & Legge, 1999).

V. WHY DO HELPERS HELP?

In this section, we explore four possible hypotheses for the evolution of helping in *N. pulcher*. Again, we emphasize that investigations into whether helpers actually help would inform us of whether investigations into why they help are necessary. Therefore, experimental demonstrations that helping benefits breeders, and field-based quantifications of the occurrence of subordinate reproduction, should be the first points of effort before tests of hypotheses explaining why helpers help are pursued. Each of the following subsections contains a review of the theoretical background, the appropriateness of *N. pulcher* as a model species to test the theory, key testable predictions to arise from each hypothesis and the empirical evidence to date. For a given hypothesis to be convincingly supported, all of the key predictions need to be met, since support for single predictions by themselves are not always sufficient to rule out alternative explanations (Table 2).

(1) Kin selection

(*a*) *Theoretical background*

Hamilton (1963, 1964*a*,*b*) formulated the concept of inclusive fitness, specifying that individuals will help kin as a means of maximizing their inclusive fitness through the attainment of indirect benefits. Since then, kin selection theory has been extensively applied to explain a wide variety of social phenomena including cooperative breeding (Emlen & Wrege, 1988; Emlen, 1991; Bourke & Franks 1995; Griffin & West, 2003; Russell & Hatchwell, 2001; Dickinson & Hatchwell, 2004; Hatchwell, 2009). Like some other cooperatively breeding species, average helper relatedness to breeders and other helpers is lower than first-order relatives (either offspring or siblings) in *N. pulcher* (Stiver *et al.*, 2005), although helpers are more closely related to breeder females than to breeder males (Dierkes *et al.*, 2005; Stiver *et al.*, 2005). High rates of breeder turnover, especially of breeder males (Stiver *et al.*, 2004), combined with helper immigration (Stiver *et al.*, 2004, 2007; Bergmüller *et al.*, 2005*a*; Heg *et al.*, 2008*a*), likely generate these low levels of within-group relatedness and the observation of decreasing relatedness with increasing helper size and age (Dierkes *et al.*, 2005; Fig. 4). Low average relatedness does not pose a problem to kin selection theory as long as average within-group relatedness (expressed as r coefficients; Queller & Goodnight, 1989) is greater than zero, which is the case for *N. pulcher* (Dierkes *et al.*, 2005; Stiver *et al.*, 2005). Even if average relatedness were zero, kin selection has the potential to drive the evolution of helping as long as some pairs of individuals within groups are related (Hamilton, 1964*a*,*b*). Therefore, *N. pulcher* has the potential to act as a good model species for investigating the potential role of kin selection in promoting helping behaviour.

(*b*) *Key predictions and tests*

Helpers use cues enabling them to distinguish kin from non-kin (Komdeur & Hatchwell, 1999). The ability to distinguish kin from non-kin, and preferentially to help kin as a result, is viewed as an important means for attaining indirect fitness benefits (Komdeur & Hatchwell, 1999; Griffin & West, 2003). Using a binary choice study, Jordan, Wong & Balshine (2009) established that *N. pulcher* helpers could discriminate between familiar individuals from their own group over unfamiliar individuals from different groups. However, helper preference could have been associated with simple familiarity rather than genetic relatedness. More conclusive support for kin recognition was provided by Le Vin, Mable & Arnold (2010), who found that sub-adults preferred to associate with unfamiliar kin over unfamiliar non-kin, and had no preference for associating with kin that were familiar *versus* unfamiliar. These results suggest that a preference for kin rather than familiarity was more important in determining shoaling preferences in *N. pulcher*.

All else being equal, more help should be given to closer relatives (Kokko *et al.*, 2002). Using data from field observations and microsatellite analyses, Stiver *et al.* (2005) found that overall levels of helping were not correlated with helper relatedness to breeder males or females within the group. However, when considering territory defence only, there was a positive correlation between territory defence and the degree of helper relatedness to breeder females (but a negative correlation between territory defence and the degree of helper relatedness to breeder males (see also Section V.2) (Table 2). This positive correlation with respect to breeder females suggests that the kin selection mechanism, if operating in this species, could be sex and behaviour specific, with helpers being selected to help related breeder females through the deployment of territory defence. Further experimental investigations are required to address this possibility. Finally, a potentially productive area of future research may entail assessment of helping effort by helpers of known genetic relatedness to breeders using pedigree data. Being certain of precise genetic relationships among individuals, as well as relying on average pairwise relatedness values, may enable more accurate and comprehensive assessments of the relationship between helping effort and relatedness.

Helpers should preferentially assist kin over non-kin (Hamilton, 1963, 1964*a*,*b*; West-Eberhard, 1975). To address this prediction, Stiver *et al.* (2005) set up laboratory groups in which helpers were either related or unrelated to both breeder males and females, and subsequently recorded the amount of help provided by helpers under both conditions. In contrast to predictions from kin selection theory, helpers in the related groups actually performed less territory defence, territory maintenance and brood chamber visits than those in the unrelated groups (see also Section V.2). However, the results of Stiver *et al.* (2005) are potentially confounded by the fact that helpers were either related or unrelated to *both* the breeding male and female within groups. Therefore, the reported motivations for helpers to help breeding females when related and breeding males when unrelated (Stiver *et al.*, 2005) were effectively set in opposition to one another. As such, further tests controlling for relatedness to one breeder while manipulating helper relatedness to the other would be useful to address this potential confound, and confirm whether helpers help breeder females to obtain kin-selected benefits. Another potential limitation is that Stiver *et al.* (2005) compared the amount of help given when helpers were either related or unrelated to dominant breeders, rather than the probability with which a given helper chooses to help a related *versus* unrelated breeder. Emlen & Wrege (1988) pointed out that the key response variable should in fact be the probability and not the amount of helping, because absolute amounts of help can be affected by many factors besides relatedness, such as the costs of helping (Heinsohn & Legge, 1999). By contrast, whether or not an individual chooses to help a related over unrelated individual, and hence the probability of helping related over unrelated breeders, should be subject to less variability and thus provide a clearer picture of individual helping preferences (Griffin & West, 2003). Therefore, future tests of kin-selected helping should employ a within-subject experimental design to assess the probability with which individual helpers help related over unrelated breeders. Such experiments have already been conducted on cooperatively breeding birds (e.g. Russell & Hatchwell, 2001), yielding the best support for kin-selected helping. Conducting such manipulations would provide a more accurate insight into whether kin selection plays a role in promoting helping behaviour in *N. pulcher.*

(*c*) *Summary*

Across vertebrates, kin selection can explain significant variation in helping behaviour, and appears to be the primary factor in some species (Bourke & Franks, 1995; Hatchwell, 2009). Experimental evidence supports kin discrimination and preferential kin association in *N. pulcher*, and positive correlations between territory defence and relatedness to breeder females provide partial support for kin-selected helping under certain conditions. However, further experiments manipulating helper relatedness to breeder females would be an important next step to confirm this possibility. Finally, the fact that experimental manipulations have revealed that related helpers do not help more than unrelated helpers suggests there is no causal role of kin selection in promoting help in *N. pulcher.* Even so, we suggest that future experiments employing a within-subject methodology designed to assess the probability with which helpers choose to help related over unrelated breeders are now required to confirm a lack of kinship effect on helping behaviour.

(2) Pay-to-stay

(*a*) *Theoretical background*

Gaston (1978) proposed that helping can serve as a payment of rent from subordinate helpers to dominant breeders, enforced by the threat of eviction by dominants. Since then, the potential benefits of rent payment by helpers have been extensively reviewed (Cockburn, 1998; Bergmüller *et al.*, 2007) and some empirical support for the model has been obtained (Reeve & Gamboa, 1983, 1987; Reyer, 1990; Reeve, 1992; Mulder & Langmore, 1993; Russell, 2004; but see Jacobs & Jarvis, 1996; Clutton-Brock *et al.*, 2005; McDonald, Kazem & Wright, 2007). Theoretical scrutiny of the pay-to-stay model has revealed that punishment is neither likely to promote the initial evolution of help nor function as the sole mechanism maintaining help (Hamilton & Taborsky, 2005). However, the pay-to-stay mechanism does have the potential to contribute to the maintenance of helping behaviour under certain plausible conditions: (1) relatedness between subordinates and dominants is low; (2) the presence of subordinates imposes costs on breeders; (3) independent dispersal and breeding is difficult and unlikely; and (4) individuals are long-lived relative to their breeding cycle (Kokko *et al.*, 2002). The social and reproductive ecology of *N. pulcher* conforms well to these conditions. Within-group relatedness is low on average (Stiver *et al.*, 2005), helpers represent competitors for social rank and are therefore likely to impose costs to breeders (e.g. Heg *et al.*, 2004*b*; Hamilton & Heg, 2008), dispersal options are limited and risky (Bergmüller *et al.*, 2005*a*; Stiver *et al.*, 2007) and individuals can live up to three years which far exceeds the length of a breeding cycle (every one or two lunar months) (Sopinka *et al.*, 2009; J.K. Desjardins, J.L. Fitzpatrick, K.A. Stiver, G. Van Der Kraak & S. Balshine, in preparation). Therefore, *N. pulcher* subordinates may potentially help as a payment of rent to dominant breeders.

(*b*) *Key predictions and tests*

Breeders punish helpers for reduced help (Gaston, 1978; Kokko *et al.*, 2002). Punishment by breeders is a critical component of the pay-to-stay mechanism (Table 2). However, punishment may go undetected if individuals behave so as to avoid its infliction. This could occur if individuals respond to the threat of punishment rather than punishment itself (Wong *et al.*, 2007). Therefore, only experimental reductions in the amount of help provided, followed by increases in breeder aggression and/or helper eviction, can be taken as firm support for this prediction. In a field experiment, Balshine-Earn *et al.* (1998) temporarily removed large, focal helpers from groups, thus preventing them from helping. Focal helpers received more aggression from other large helpers (but not breeders) upon their return to the group, suggesting that focal helpers may have been punished by other helpers. Indeed, this experiment has become widely cited as experimental evidence for the punishment of helpers (e.g. Bergmüller *et al.*, 2007; Sachs & Rubenstein, 2007; Hochberg, Rankin & Taborsky, 2008; McDonald *et al.*, 2008; but see Balshine & Buston, 2008; Field & Cant, 2009).

Closer examination of the patterns of aggression in the Balshine-Earn *et al.* (1998) study in fact suggests that the increased aggressiveness was more likely a result of intensified conflict over rank between helpers (Field & Cant, 2009), since only helpers of the same size and sex as the focal helpers became more aggressive (Balshine & Buston, 2008). Furthermore, while some focal helpers were reportedly 'evicted' owing to their subsequent disappearance from the group, evictions were never actually observed making it impossible to confirm that the disappearances were a product of forcible eviction rather than predation or voluntary departure. Even if helpers were evicted, the most likely perpetrators would have been other large helpers of the same size and sex as the focal helpers given that eviction is usually preceded by elevated rates of aggression from similar-sized group members in this and other species (Dierkes *et al.*, 2005; Wong *et al.*, 2007). Any evictions would therefore have been more likely to arise due to conflict over rank rather than as punishment for reductions in helping effort.

The experiment by Balshine-Earn *et al.* (1998) was also unable to separate out the effects of reduced helping effort from helper absence from the group. Using a clever laboratory experiment, Bergmüller & Taborsky (2005) disentangled these factors by preventing helpers from helping (*via* territory defence) whilst allowing them to remain present within their social group. As in the Balshine-Earn *et al.* (1998) study, focal helpers that had been prevented from helping did not receive more aggression from breeders than helpers that were allowed to help. In addition, focal helpers did not receive more aggression from large helpers, although these focal helpers displayed more submission towards large helpers. This pattern (no change in aggression received but an increase in submission given) led Bergmüller & Taborsky (2005) to suggest that helpers may be using submissive and helping behaviours as a means of pre-emptively appeasing their dominants. According to Bergmüller & Taborsky (2005), helpers may have thus prevented the infliction of punishment through the excessive use of submission and help. While this interpretation is appealing, the data actually suggest a different explanation. The amount of total appeasement (submission plus helping) given was positively correlated with the amount of aggression received, implying that submission serves to appease dominant aggression (since the more aggression one receives, the more submission one has to provide). If on the other hand, a helper is effectively *pre*-emptively appeasing a breeder with submission and help, one would actually expect to see that the more total appeasement behaviour given the less aggression received, and thus a negative correlation between these two factors. Therefore, we suggest that evidence for pre-emptive appeasement is currently inconclusive, and that further experimental manipulations of helper submissiveness and examinations of potential punitive responses by breeders are required. Until then, the most convincing and parsimonious explanation for the lack of detectable punishment by breeders in both studies is that helpers simply do not face the threat of punishment in *N. pulcher*.

Punishment leads to increased help (Clutton-Brock & Parker, 1995). The field study by Balshine-Earn *et al.* (1998) and the laboratory study by Bergmüller & Taborsky (2005) both demonstrated that helpers that had been prevented from helping subsequently elevated their helping efforts above previous levels. It is tempting to assign such increases in helping effort to the threat of punishment—but since neither study reported any increases in breeder aggression, and the evidence for pre-emptive appeasement is debatable, it seems unlikely that the increased helping efforts by helpers were a response to the threat of breeder punishment. Alternative explanations for the increased helping efforts do exist, for example, helpers may have helped more to compensate for any reduced social prestige they would have incurred as a result of being absent from the group and thus not helping. Such plausible alternatives for why helpers helped more should not be neglected, and attempts made to test them in the future.

Punishment for not helping scales positively with the need for help (Mulder & Langmore, 1993). Punishment (in the form of aggression, policing or eviction) has costs (Clutton-Brock & Parker, 1995) and hence dominant breeders are only expected to punish when they need but do not receive help. If punishment scales with the need for help, a key test would be to show that helpers prevented from helping when the need for help is great receive more punishment than when the need for help is small. To date there have been no direct tests of this prediction in *N. pulcher*. Bruintjes & Taborsky (2008) came close by experimentally manipulating the need for help in the laboratory by subjecting *N. pulcher* groups to treatments with a high and low density of conspecific intruders. Helpers exhibited more defence in the high- compared to low-density treatments, which could, as Bruintjes & Taborsky (2008) suggest, demonstrate that the amount of help given was based on the need for help by breeders. However, this explanation relies on the assumption that breeders benefit from helping, which has yet to be convincingly demonstrated. A more parsimonious, alternative explanation for this result could be that helpers need to exhibit more defence in the high-density treatment simply because they have to defend their position in the breeding queue from more potential competitors. Finally, since helpers were not prevented from helping under a high and low density of intruders in this study, it can not be ascertained whether the occurrence or degree of punishment for not helping scaled with the breeder's need for help.

Less help should be given to closer relatives (Kokko *et al.*, 2002). Stiver *et al.* (2005) demonstrated that overall levels of helping effort were not correlated with relatedness to breeder males or breeder females. However, when considering territory defence alone, there was a negative correlation between territory defence and relatedness to breeder males. In other words, when less territory defence was given there was higher relatedness between helpers and breeder males, in support of the prediction. This result indicates that the pay-to-stay mechanism, if operating in this species, could be sex- and behaviour-specific, with helpers using territory defence as a payment to breeder males to stay. Additionally, the fact that helpers in unrelated groups helped more than helpers in related groups also supports this prediction, however, as mentioned in Section V.1, helpers were set up to be related or unrelated to both breeder males and females thus introducing a potential confound to the study.

Helpers should be less helpful when breeders are absent (McDonald *et al.*, 2008). According to the pay-to-stay model, helpers that signal their helpfulness avoid punishment by breeders and thereby gain access to the safety of the group and territory. Therefore, the removal of the intended audience (the dominant breeders) should result in the cessation of help given (Wright, 1997; McDonald *et al.*, 2008) (Table 2). Thus, the pay-to-stay hypothesis and the signals of prestige hypothesis (see Section V.3) both assume that any positive effects of help on breeder or offspring fitness are irrelevant from the helper's perspective. The helper is only concerned with the benefits accrued from signaling its helpfulness, and thus these two hypotheses are explicitly connected. This prediction has yet to be tested in *N. pulcher*.

(*c*) *Summary*

Among the various adaptive explanations for help, the pay-to-stay hypothesis has attracted the most empirical attention in *N. pulcher* with six studies specifically addressing this hypothesis to date (Fig. 1B). However, the key prediction, that breeders punish absent or lazy helpers has never been demonstrated despite the appropriate tests being conducted. While the occurrence of pre-emptive appeasement would support the occurrence (but invisibility) of punishment, patterns of submission, help and aggression currently suggest that helpers are unlikely to appease pre-emptively. The fact that punishment by breeders has not been detected renders any support for the pay-to-stay hypothesis based on the other key predictions largely tenuous. Until punishment or pre-emptive appeasement can be convincingly demonstrated through careful experimental manipulation, the evidence as it stands suggests that helpers do not face the threat of punishment for not helping in *N. pulcher*. Hence helping behaviour is unlikely to have evolved or be maintained as a payment of rent in *N. pulcher*.

(3) Signals of prestige

(*a*) *Theoretical background*

Zahavi (1974) proposed that exaggerated traits function as handicaps, providing honest signals of individual quality. The elegance of his 'Handicap Principle' derives from its implicit integration of costs—a signal is selected for precisely because it reduces the fitness of its bearer. Higher quality individuals can better afford the costs of advertising than lower quality individuals, resulting in reliable correlations between signal magnitude and intrinsic quality (Grafen, 1990). Later, Zahavi (1995) proposed that altruistic behaviour could serve as one such costly advertisement of quality, with helpers gaining from helping by enhancing their prestige within the group. High social prestige would be beneficial for gaining collaborators, increasing dominance rank and ultimately for acquiring reproductive opportunities. These direct benefits would thereby promote the evolution and stability of helping as a signal (Gintis, Smith & Bowles, 2001; Lotem, Fishman & Stone, 2003).

From the outset, it seems feasible to expect that help in *Neolamprologus pulcher* could serve a signaling function given that help has an energetic cost (Grantner & Taborsky, 1998; Taborsky & Grantner, 1998), individuals vary in quality (Fitzpatrick *et al.*, 2006), and individuals compete with each other over reproduction (Heg *et al.*, 2006, 2008*b*). However, it is unclear whether helping would be selected for as a signal of quality when there are other un-cheatable quality indicators already present in social groups of these fish. Like in many other animal societies, *N. pulcher* groups are organized into dominance hierarchies in which individuals are ranked based on some observable trait, in this case body size (Heg *et al.*, 2004*b*; Fitzpatrick *et al.*, 2008). Therefore, within such hierarchies, an individual's body size (and hence dominance rank) would provide the most reliable and efficient cue of their quality. As such, any individual would be able to assign intrinsic quality simply through assessing the body size and hence rank of other group members, rendering the need for exaggeration of an additional trait like helping effort as a signal for quality unnecessary. Indeed, Zahavi (1995), Grafen (1990) and Gintis *et al.* (2001) specify that the ability to observe the quality of interest negates the need for help as a signal.

Another potential theoretical problem with the signal of prestige model was pointed out by Wright (2007). Benefits as well as costs are accrued from helping, and these benefits are likely to vary among individuals. For example, if breeders benefit from help, a related helper will have greater potential benefits from helping than an unrelated helper owing to indirect benefits (Hamilton, 1964*a*,*b*). All else being equal, the related helper is likely to help more (or with higher probability) than an unrelated helper, even though both helpers may be of similar quality and hence be able to bear the same costs of helping. Inter-individual variation in the benefits accrued from helping, irrespective of the costs individuals can bear, can therefore lead to variation in the amount of helping effort. Under these circumstances, receivers hoping to use helping as a signal of prestige, and thus as an indication of the costs a helper is able to bear, would have to discount the effects of varying benefits and essentially calculate the amount of remaining helping effort that could be functioning solely as a signaling component (Wright, 2007). In theoretical treatments of altruism as a signal of quality (Gintis *et al.*, 2001; Lotem *et al.*, 2003), the benefits of help were assumed to remain constant. Hence, mathematical modeling incorporating individual variation in the benefits of help as well as dominance relationships within groups would be an important next step in addressing the validity of this hypothesis for species like *N. pulcher*.

(*b*) *Key predictions and tests*

The level of help provided should influence the probability of being chosen as a mate, collaborator or competitor (Zahavi, 1995). Breeder-removal experiments under natural conditions have demonstrated that more helpful female helpers are more likely to inherit breeding status within the group (S. St-Cyr, M.Y.L. Wong, S.R. March-Rollo, J.O. Reynolds, N. Aubin-North & S. Balshine, in preparation). However, such trends are not conclusive because alternative explanations, including the fact that high-quality helpers may be both able to help more and inherit breeding status, could be invoked. Therefore, levels of help that helpers provide would need to be experimentally manipulated [see Bergmüller & Taborsky (2005) for a methodological example] and any resulting behavioural changes monitored in all other group members. Helpers prevented from helping (and thus signaling) would be expected to receive increased aggression and less social affiliation than helpers allowed to help, as well as experience a reduced likelihood of inheriting breeding status, since helpers that do not signal through helping are more likely to be viewed as poorer quality competitors, mates or collaborators (Table 2). To date, no such investigations have been conducted in *N. pulcher*.

Helpers should be less helpful when they do not have an audience (Wright, 1997). Under the signal of prestige hypothesis, helpers are motivated to provide help in order to signal their underlying quality rather than to increase the reproductive output of breeders. As for the pay-to-stay hypothesis (see Section V.2), helpers should therefore reduce the levels of help they exhibit when breeders or other intended recipients of the signal are absent (Table 2). To date, no such investigations have been conducted in *N. pulcher*.

The degree to which help is exaggerated should be positively related to the quality of the signaler (Lotem, Wagner & Balshine-Earn, 1999). Before examining this correlation, one would have to verify that observed levels of help are indeed an exaggeration of helping effort beyond that intended to accrue other direct or indirect benefits of helping. If helping is exaggerated to function as a signal of quality, residual help levels (after accounting for helping effort due to other factors) could be correlated with a measure of individual quality. For example, if helpers also help to obtain indirect, kin-selected benefits, one could plot the residuals of a regression between relatedness and helping effort against a measure of individual quality, expecting a positive correlation between the two. On the other hand, if there are no other known benefits of helping, then absolute help levels and measures of individual quality could be correlated. Using field data on helping effort in *N. pulcher*, Stiver *et al.* (2005) found that two potential proxies of individual quality, namely body size and dominance rank, did not explain a significant amount of variation in absolute levels of help, suggesting that absolute levels of help do not correlate with individual quality as predicted. Further investigations examining correlations between residual help levels and individual quality would be useful to test this prediction.

(*c*) *Summary*

From a theoretical perspective, the signal of prestige model may have limited applicability in species such as *Neolamprologus pulcher* that exhibit well-defined size-based dominance hierarchies and where the benefits of helping may vary considerably among individuals. From an empirical perspective, there have been no direct tests of any of the key predictions of the model in *N. pulcher*. Our understanding of the role of signaling in promoting help in *N. pulcher* is therefore in its infancy, and would benefit from further modeling of the effects of varying benefits of help and dominance relationships on the evolutionary stability of help as a signal of prestige, and carefully designed experimental tests of each of the key predictions of this hypothesis.

(4) Group augmentation hypothesis

(*a*) *Theoretical background*

Woolfenden (1975) first proposed that helping could be favoured if it enhances group size which in turn increases helper survival and future reproductive output. Helper fitness could be enhanced either *via* the accrual of passive group-augmentation benefits (*via* the simple presence of other group members) and/or by active group-augmentation benefits (*via* help provided by other group members) (Kokko *et al.*, 2001). The evolutionary stability of both types of group augmentation were modeled by Kokko *et al.* (2001) who showed that helping to obtain an augmented group could occur under the following restrictive conditions: (1) helpers can eventually inherit breeding status within the group; (2) at least some of the offspring that a helper helps to rear are retained within the group; (3) helpers incur survival costs from helping and these costs accelerate with the amount of help given; (4) immediate survival costs of helping are less than the long-term survival benefits from inheriting a large group; and (5) other group members do not fully compensate for any help not provided by helpers. There have been no attempts to quantify the survival costs or cost functions of helping in *Neolamprologus pulcher*, therefore assumptions 3 and 4 can not be verified. However, it is known that helpers can inherit breeding status within the group (Stiver *et al.*, 2006), supporting assumption 1, and that helpers do not fully compensate for reductions in help levels when other helpers are removed from the group (Brouwer *et al.*, 2005), supporting assumption 5. Hence it remains possible that *N. pulcher* will be a suitable model species for testing Kokko *et al.*'s (2001) version of the evolution of helping due to group augmentation.

(*b*) *Key predictions and tests*

Helping increases breeder productivity (Kokko *et al.*, 2001). In *Neolamprologus pulcher*, the number of young emerging (Balshine *et al.*, 2001) and surviving (Brouwer *et al.*, 2005) is positively related to the number of helpers within a group. While these results have been cited as evidence that help increases breeder productivity (e.g. Balshine & Buston, 2008; Desjardins *et al.*, 2008*b*), we in fact do not know whether enhanced breeder productivity is a consequence of the presence of helpers, helping itself, or a combination of both. To assess directly whether helping effort increases breeder productivity, experimental tests in which helpers are prevented from helping, or statistical tests that account for the effects of both group size and help levels on breeder productivity, are needed (see also Section III.2). Furthermore, since territory quality (as determined by territory size and number of shelters) is also correlated with group size in this species (Balshine *et al.*, 2001), future studies should ensure that territory quality is controlled for when investigating the effects of helping and helper number on breeder productivity.

Increased breeder productivity leads to greater recruitment of offspring back to the group (Kokko *et al.*, 2001). Increased breeder productivity will enhance recruitment back to the group as long as some offspring remain philopatric (Kokko *et al.*, 2001). Molecular data has demonstrated that within-group relatedness is greater than between-group relatedness in *N. pulcher* (Dierkes *et al.*, 2005; Stiver *et al.*, 2008), implying a degree of natal philopatry in this species. To provide more direct evidence of this link, breeder productivity at time t would have to be correlated with the change in group size between t and time $t + 1$ (group size at $t + 1$—group size at t). A positive correlation between breeder productivity at time t and change in group size would be expected if enhanced breeder productivity leads to increased recruitment back to the group. In a long-term field study, Heg *et al.* (2005) found that the size of a group in one year was positively related to the size of that group the following year. However, it is unclear whether large groups arose due to increased breeder productivity in large groups the previous year since breeder productivity was not measured. In addition, since individual group members were not marked and could not be re-identified, it remains unclear whether large groups were also large the following year because they had greater recruitment than small groups. Group size correlations between years may simply have arisen because of habitat differences, whereby good territories support large groups and such good territories are likely to remain of high quality across years. Further long-term field studies monitoring breeder reproductive success and recruitment to the group are needed to provide conclusive evidence that increased breeder productivity results in increased recruitment in *N. pulcher*.

There are benefits of living in a larger group (Kokko *et al.*, 2001). Several studies have examined the consequences of living in groups of different size in *Neolamprologus pulcher*. Breeders and helpers residing in larger groups benefit in terms of increased survival (Heg *et al.*, 2004*a*, 2005) and reduced predation risk (Balshine *et al.*, 2001). Breeders (but not helpers) in large groups had increased feeding rates (Balshine *et al.*, 2001; Brouwer *et al.*, 2005), reduced workload (Balshine *et al.*, 2001) and increased number of offspring produced and surviving (Balshine *et al.*, 2001; Brouwer *et al.*, 2005; Taborsky, 1984). While the benefits of living in larger groups are well documented, it would be useful to determine whether these benefits are passively or actively accrued (Kokko *et al.*, 2001). The relative effects of passive *versus* active processes could be distinguished by statistically accounting for the effects of both group size (addressing passive effects) and help given (addressing active effects) on the magnitude of group-size-related benefits that helpers obtain. To date, no such investigations have been conducted in *N. pulcher*.

(*c*) *Group augmentation and the trait group selection perspective*

The group augmentation hypothesis has recently received attention under the guise or misnomer of “new” or “trait” group selection (Wilson, 1998, 2006). Although long ago, Williams (1966) and Maynard Smith (1964) put to rest the “good-for-the-species” flavour of group selection advocated by Wynne-Edwards (1962), the term has been resurrected (Wilson, 2008). A number of authors have argued that whenever the competition among groups (global competition) is stronger than competition within groups (local competition), helping or cooperation can be selected for by group selection (Wilson, 1975, 2008; Keller & Reeve, 1999; Korb & Heinze, 2004; Bowles, 2006; Boyd *et al.*, 2003; Wilson & Wilson, 2007). The premise is that groups of cooperators will do better than groups of selfish individuals and hence helping can be selected despite the fact that helping is costly to the individual helper at a within-group level. Hence the terms group selection (Wilson, 2008) or multi-level selection (Keller & Reeve, 1999) have been evoked. However, this type of “group selection” in fact relies on the inclusive fitness benefits accruing to those who are being “altruistic”. At the level of global competition with all other individuals in the population, a helpful individual is better off as a result of their help because their group is stronger, larger, more competitive, and better fed, and hence its individual fitness increases (Lehmann & Keller, 2006; West, Griffin & Gardner, 2007). Essentially this is the group augmentation mechanism (an individual benefit) discussed above. So helpers themselves often benefit directly from the help provided to the entire group, even though other members of their group may benefit even more from their help. Note that selection for cooperation is still operating at the level of the individual. Typically the other group members that benefit will be kin due to the low gene flow in most social groups. Hence, apparent arguments of group-level selection for help can be more parsimoniously explained *via* individual-level inclusive fitness benefits (Reeve, 2000; West *et al.*, 2007). One potentially useful avenue for research with *N. pulcher* would be to examine whether global competition is greater than local competition, and if so, one would expect that individuals in groups with more helping have higher fitness than individuals in other groups with less helping.

(*d*) *Summary*

The key predictions and tests of the group augmentation model have rarely been made explicit. Essentially, what is required is to demonstrate that helping boosts group size and that large group sizes provide future benefits (passive and/or active) to helpers. There is now convincing empirical evidence to suggest that *Neolamprologus pulcher* helpers benefit from residing and eventually breeding in large groups. However, empirical support for other key predictions of the group augmentation model, as well as the survival cost assumptions of the model (Kokko *et al.*, 2001) are decidedly lacking and should be the focus of future research attempts.

VI. FUTURE DIRECTIONS

Our review clearly reveals that many important questions remain to be addressed. We propose that the following key areas of research deserve particular attention in the future if we are finally to elucidate the adaptive significance of help in *N. pulcher* and in other species.

(1) Long-term studies of marked individuals

Many of the key breakthroughs in cooperative breeding research have come from long-term studies of marked individuals in birds and mammals (e.g. Reyer, 1984; Dickinson, Koenig & Pitelka, 1996; Richardson, Burke & Komdeur, 2002). We therefore propose that future research in *N. pulcher* should involve long-term observations of marked individuals. This species is particularly amenable to such investigations because individuals are site-attached, facilitating the repeated relocation of groups of individuals within distinct sub-populations over time, and well-established techniques exist for the long-term tagging of small-bodied fish (Munday & Wilson, 1997).

One key direction for future long-term studies should be the quantitative assessment of the inclusive fitness effects of helping for helpers and breeders. Previous research on helping in *N. pulcher* has largely assumed that helping is initially altruistic, imposing a net cost on donors, but ultimately confers a net benefit to donors. Studies have also implicitly assumed that help must confer a net benefit for the recipient (the breeders). However, to ascertain whether helpers actually help, the costs and benefits of helping for both helpers and breeders need to be quantified using an accurate proxy of inclusive fitness i.e. reproductive success (Table 3). Furthermore, by quantifying the costs and benefits to helpers and breeders in this way, we can determine whether benefits to helpers are primarily direct or indirect (Table 3). As it currently stands, we still know surprisingly little about the basic pay-offs of helping for helpers and breeders. Long-term studies of marked individuals, such as those conducted in other taxa (Reyer, 1984; Emlen, 1991; Dickinson *et al.*, 1996; Richardson *et al.*, 2002; Oli & Armitage, 2003), would therefore be invaluable for quantifying the inclusive fitness benefits of helping for helpers and breeders in *N. pulcher*, whilst controlling for multiple aspects of breeder and territory quality.

Long-term studies of marked individuals, combined with genetic analyses of parentage, should also be directed towards determining the relative frequency of subordinate reproduction within groups, thus enabling investigations into whether helpers are simply serving their own selfish interests by providing ‘help’ (see Section III.1).

(2) Distinguishing the fitness effects of helping from helper presence

As yet, whether helping *per se* has a positive effect on breeder fitness is not known because any effects of helping have been confounded by the removal of helpers from the group (Buston & Balshine, 2007). Fitness effects of helping could be demonstrated experimentally, by employing careful experimental techniques in which helpers are allowed to remain in their groups but are not allowed to help [see Bergmüller & Taborsky (2005) for such an example], or whenever possible controlled for statistically, by separately analyzing the effects of helper number and helping effort on breeder reproductive output whilst controlling for differences in territory quality (Emlen, 1991) and maternal effects (Russell *et al.*, 2007; Taborsky *et al.*, 2007; Russell & Lummaa, 2009).

(3) Tests of the key predictions of the adaptive explanations for helping

Assuming that helpers do indeed help, we need to turn our attention to the next important question: why do they help? Over three decades of research, there has been significant progress made in understanding helping and social behaviours in *N. pulcher*; however, our understanding of whether and why helpers help is still incomplete. While efforts should be made to test the key predictions of each hypothesis (see above and Table 2), we suggest that the following tests should represent the next phase of research for each hypothesis: (*a*) *kin selection*: within-subject choice tests should be conducted comparing the probability that a given helper chooses to help a related breeder over an unrelated breeder. (*b*) *Pay to stay*: further experimental tests are required to address the function of submissive and helping behaviours, and to investigate alternative explanations for increased help following removal from the group or prevention from helping. (*c*) *Signals of prestige*: theoretical explorations of the evolutionary stability of help as a signal of prestige when individuals are organized into dominance hierarchies and where benefits of help are allowed to vary among individuals, and empirical demonstrations of reduced helping effort in the absence of a relevant audience. (*d*) *Group augmentation*: demonstrations of positive associations between levels of helping, number of offspring surviving (breeder productivity) and changes in group size.

(4) Assessing the relative contributions of the adaptive explanations for helping

From an empirical perspective, tests of the pay-to-stay hypothesis have outnumbered those for other mechanisms, particularly the signal of prestige hypothesis (Fig. 1B). If we are to gain a more thorough understanding of the relative importance of the different hypotheses for helping, a key priority should be to reduce the skew in empirical studies by focusing future empirical investigations on the under-studied hypotheses for helping behaviour and the remaining key predictions of each hypothesis.

From a theoretical perspective, it is generally assumed that the different hypotheses for help are not mutually exclusive. However, while the various hypotheses may have the potential to act concurrently, whether they actually do so will not be clear without theoretical modeling that simultaneously incorporates the effects of each of the mechanisms (H. Kokko, personal communication). For example, if helpers help voluntarily (i.e. due to the benefits accrued *via* kin selection, group augmentation or signals of prestige), would breeders need to use coercive actions (i.e. punishment and the pay-to-stay mechanism) to enforce helping? Thus, while help due to pay-to-stay may select for helping in the absence of other mechanisms promoting help, if there are other mechanisms selecting for helping in operation, and if they contribute greatly to the fitness of individual helpers, then it is unclear whether pay-to-stay forces further selects for or maintains helping behaviour. Kokko *et al.* (2001, 2002) have already made progress in modeling multiple mechanisms, namely kin selection and group augmentation (Kokko *et al.*, 2001), and kin selection and pay-to-stay (Kokko *et al.*, 2002). Further models incorporating a greater range of or all of the different mechanisms at once would be important as a means of defining the parameter spaces in which certain mechanisms may become redundant in the presence of other mechanisms promoting and maintaining help. Another useful avenue would be to employ the now widely applied information-theoretic approach with Akaike information crierion (AIC) (Burnham & Anderson, 2002) to test alternative models within the same statistical framework, and thus provide support for or against a given set of predictions within a single modeling framework (Richards, 2005).

(5) Variation in helping effort

Understanding the causes and consequences of inter-individual variation in helping effort is important if we are to elucidate fully the adaptive significance of helping behaviour (Magrath, 2001; Clutton-Brock *et al.*, 2002; Cant & Field, 2005; Field, Cronin & Bridge, 2006). There are at least three factors that could contribute to variation in helping effort: helper sex, size and social rank. Various studies have addressed the effects of helper sex (Stiver *et al.*, 2005), size (Taborsky, 1984; Bergmüller & Taborsky, 2005; Bergmüller, Heg & Taborsky, 2005*b*; Stiver *et al.*, 2005; Brouwer *et al.*, 2005; Bruintjes & Taborsky, 2008; Heg *et al.*, 2009) and rank (Stiver *et al.*, 2005) on general patterns of helping behaviour or helper responses to experimental manipulations in *N. pulcher*. Acknowledging variation in these factors is important because the existence of variation means that averaging helping effort across all helpers may obscure true patterns of helping behaviour and inhibit our understanding of its adaptive significance. In addition, we also propose that a formal theoretical framework is needed which predicts how variation in sex, size and rank may influence the propensity to help under each of the hypotheses for helping behaviour. Such a framework should integrate each of the key hypotheses for helping behaviour, and under each hypothesis, generate testable predictions of how patterns of helping are likely to vary depending on the sex, size and rank of helpers. While enabling us to clarify how help varies as an independent or collective function of these factors, an integrated framework would ultimately serve as a novel and complimentary means by which we can elucidate the ultimate reasons for why helpers help.

(6) Altruism *versus* mutualism?

Historically in the *Neolamprologus pulcher* literature, brood care, territory maintenance and territory defence have been considered altruistic forms of cooperation. Following Bergmüller *et al.* (2007) and Buston & Balshine (2007), we define behaviours as an altruistic form of cooperation if they impose a net cost, at least temporarily, on helpers that is later compensated by various direct and/or indirect benefits (Fig. 6). The proposition that such behaviours may alternatively reflect mutualistic forms of cooperation, imposing no initial net cost to helpers, has never been raised, which is surprising given that mutualisms have been widely documented in other social species that exhibit collective defence or maintenance of territories (Gross & MacMillan, 1981; Clutton-Brock, 2002, 2009; Olendorf, Getty & Scribner, 2004). Behaviours can be defined as mutualistic if they raise the absolute fitness of both individuals, and if each individual does even better by coordinating their activities rather than performing them alone (West *et al.*, 2007; Fig. 6). Therefore, there is no temptation to defect, at least for immediate mutualisms (referring to mutualisms where the benefits to both individuals are reaped immediately rather than with delay), and there is no mystery in explaining the evolution of non-costly, mutualistic cooperation unlike costly, altruistic cooperation. Clearly, differentiating between mutualistic and altruistic cooperation is of importance to empiricists, because only for altruistic cooperation would we need to assess the evolutionary mechanisms that eventually compensate for the cost they impose. Ideally, distinguishing between mutualistic and altruistic cooperation would require quantification of the pay-off matrix associated with cooperation *versus* defection (Dugatkin, 2002). Quantification of the pay-off matrix pertaining to cooperative behaviours, while the ultimate goal, may be difficult to achieve empirically. As such, we here suggest alternative, indirect means by which we could identify whether a behaviour has the potential to be mutualistic as opposed to altruistic.

With regards to broodcare in *Neolamprologus pulcher*, whether it could be regarded as mutualistic, altruistic or even selfish could be inferred depending on whether helpers themselves have engaged in direct reproduction. Broodcare by helpers could potentially reflect selfishness if broodcare is directed only towards their own young (see Section III.1), mutualistic if both helpers and breeders care for their own and each other's young, or altruistic if helpers do not reproduce but help rear the breeder's young. To address these possibilities, future research should aim to quantify in the field the relative frequency with which helpers *versus* outsider conspecifics gain maternity or paternity in the

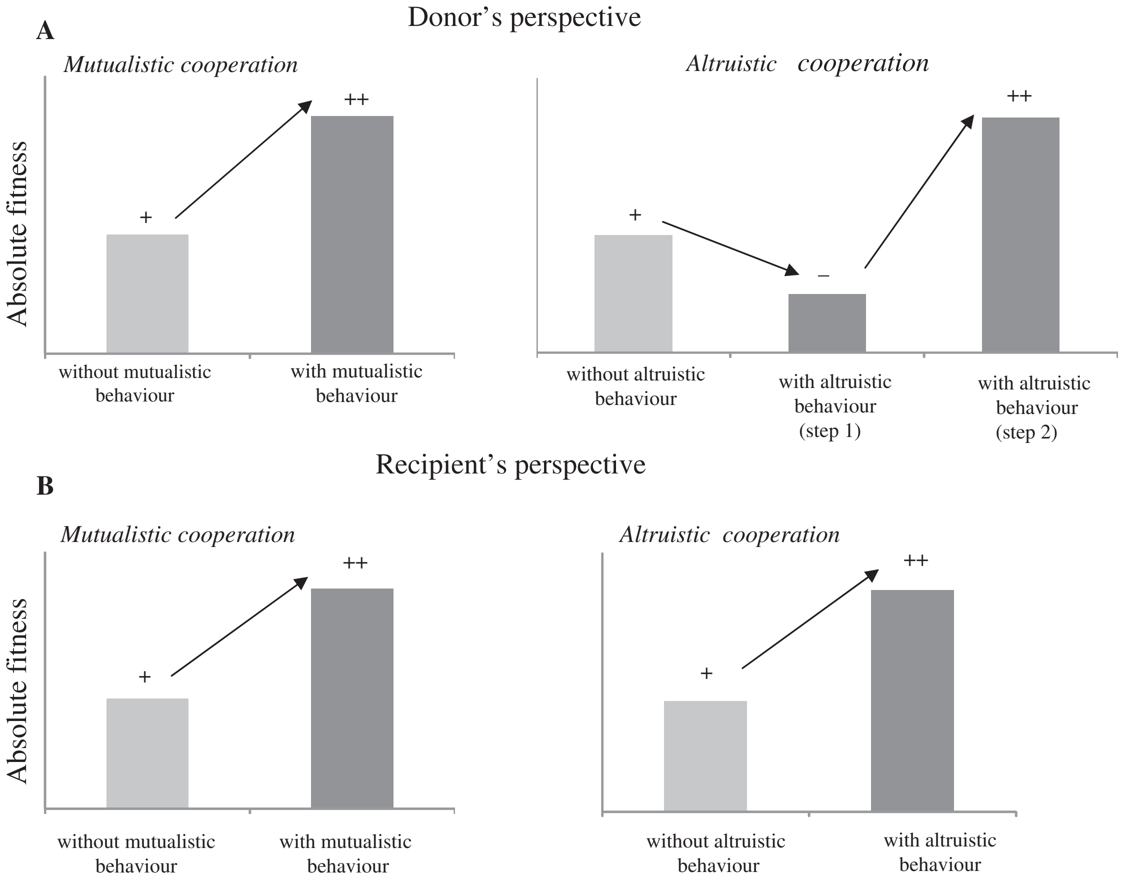

Fig. 6. Fitness pay-offs under mutualistic and altruistic cooperation for (A) donors and (B) recipients of the behaviour. All individuals ultimately experience increases in absolute fitness from the behaviour (+ to ++). However only when employing altruistic behaviours do donors experience a reduction in absolute fitness, at least temporarily. Thus only with respect to altruistic cooperation do compensatory benefits (indirect or direct) subsequently need to be invoked in order to explain the evolution of the behaviour. Note that mutualistic cooperation is a two-way street, with both individuals essentially acting as donors and recipients of the behaviour. Altruistic cooperation may be two-way or one-way.

broods. Additionally, since the egg clutches of breeder and helper females can reliably be distinguished from each other in the laboratory (Heg *et al.*, 2009), future work comparing the relative frequency with which helper and breeder females provide broodcare to their own brood over the other female's brood would serve as a useful indication of the degree to which broodcare is selfish, mutualistic or altruistic.

With respect to territory maintenance (the removal of sand and debris), whether or not it is mutualistic, altruistic or selfish could potentially be inferred from the area of the territory that helpers maintain and use. Helpers in *N. pulcher* typically remain in a small sub-territory within the larger group's territory (Werner *et al.*, 2003). Territory maintenance could be altruistic if helpers maintain the brood chamber occupied by breeders and their offspring but primarily use other shelters in their sub-territory as protection from predators. Alternatively, it could be regarded as mutualistic if individuals primarily maintain shelters within their own sub-territories yet also use shelters maintained by other group members. In addition, due to the network of shelters excavated under stones, helpers maintaining shelters within their own sub-territories may actually be contributing to the maintenance of the entire shelter network and thus behaving in a mutualistic fashion. Finally, territory maintenance could be viewed as selfish if helpers only maintain and use shelters located within their own sub-territories and never maintain the brood chamber. To assess whether helpers are behaving altruistically, selfishly or mutualistically, future investigations would therefore benefit from quantifying the relative frequency with which helpers maintain and use their own shelters, other shelters or the brood chamber within the group territory.

Finally, whether or not territory defence should be considered mutualistic or altruistic could be inferred by the type of intruders repelled and the location at which defence occurs. Territory defence may reflect a form of strict cooperation when directed towards potential egg predators, but potentially mutualistic when directed to predators of adults, scale parasites or intruding conspecifics. Furthermore, territory defence could be considered selfish if it is conducted primarily in a helper's sub-territory, mutualistic if conducted anywhere else in the group territory, or strictly cooperative when conducted predominantly in the brood chamber. Future empirical investigations would therefore benefit from assessing the nature and spatial location of territory defence.

(7) New technologies

Throughout this review, we have focused on understanding helping from an ultimate perspective in terms of its adaptive significance for helpers and breeders. In addition, we argue that new technical advances in genetics and neurobiology make this an especially fruitful time to investigate helping behaviour using an integrative and comprehensive framework. A fertile growth of neuroscience and neurobiology over the last few decades has generated many techniques readily applicable to understanding behaviour in non-human vertebrates, including immunocytochemistry, *in-situ* hybridization, intra- and extracellular electrophysiological recording, and neuroimaging of the neurochemical circuits of the brain. These tools can provide insight into how the brain changes during complex social behaviour such as helping, providing a more comprehensive understanding of the evolution of cooperation, group dynamics and social behaviour. While the neural-physiological mechanisms underlying variation in cooperation and social conflict to date remain largely unexplored, recent studies are starting to pave the way by examining individual variation in hormone and neuropeptide profiles in relation to sex and social status (Buchner, Sloman & Balshine, 2004; Desjardins *et al.*, 2006, 2008*a*,*b*; Aubin-Horth *et al.*, 2007; Bender *et al.*, 2008; Mileva *et al.*, 2009; Taves *et al.*, 2009).

In this review, we have argued that experimentally to unravel the mechanisms responsible for cooperative behaviour, we must manipulate the level of helping effort and explore the fitness consequences of such actions. While the brain-imaging techniques described will help us pinpoint what areas or brain centres are involved in modulating helping behaviour, these techniques do not allow for manipulation of behaviour. To do so, it may be possible to alter helping levels without manipulating helper number by applying hormones (estradiol, testosterone), neuropeptides (isotocin or prolactin) or blockers of these chemical signals (Kobayashi, Aida & Stacey, 1991; Oliveira *et al.*, 2001; Yamaguchi *et al.*, 2004; Serrano *et al.*, 2008; Ziegler *et al.*, 2009). Such neuro-endocrinological manipulations have the potential to provide a large step forward towards achieving a comprehensive understanding of social evolution.

Additionally, the fields of genomics and sociogenomics have expanded over the last decade, with large-scale genome-sequencing projects being undertaken. A number of fish species, such as puffer fishes (*Takifugu rubripes* and *Tetraodon nigroviridis)* (Aparicio *et al.*, 2002) have been sequenced, and other fish species such as the stickleback, *Gasterosteus aculeatus* (Leder, Merila & Primmer, 2009), the zebrafish *Danio rerio* (Amores *et al.*, 1998), salmon (McClelland & Naish, 2008) and some cichlids are scheduled to have their sequences completed in the near future. These fish genome projects will no doubt provide information about which patterns and networks of genes are likely to be involved in social behaviours including cooperative behaviours. Whole-genome-sequence studies are being followed by target gene function studies. Genetic knock-in or knock-out experiments, specific to one or several genes important in social behaviour, are currently being developed and used to investigate cooperative social behaviour (Ophir, Wolff & Phelps, 2008; Young *et al.*, 1999; Lim *et al.*, 2004; Donaldson & Young, 2008). If particular targeted knock-in or knock-out individuals do not express social and cooperative behaviours to the same extent as normal controls, we would then be able to examine experimentally the effect of the absence of cooperation on donors and recipients. Hence by combining classical behavioural studies with new molecular techniques, we will gain a much more solid scientific foundation for understanding the molecular and genetic mechanisms underlying cooperative behaviours such as helping.

VII. CONCLUSIONS

(1) Three decades of research on *N. pulcher* has spawned considerable work on both cooperative and other behaviours, and has significantly enhanced our understanding of whether and why helpers help. Even so, more research is still required to provide a clearer understanding of helping behaviour in this species.

(2) Here we emphasize that while broad patterns of helping behaviour have emerged, we still require a better appreciation of the basic pay-offs of helping to helpers and breeders, a cohesive theoretical framework that incorporates all the potential mechanisms of helping behaviour, empirical tests of all the key predictions pertaining to each proposed mechanism for helping and an understanding of their relative importance.

(3) To pinpoint which of the adaptive explanations could be responsible for helping in this species, concise and critical evaluations of the key remaining predictions of each mechanism need to be employed, combined with long-term field investigations of the inclusive fitness of helping for helpers and breeders.

(4) We propose the possibility that some ‘helping’ behaviours, usually assumed to represent altruistic cooperation, may represent mutualistic forms of cooperation and even selfishness and thus may not require examination in light of the conundrum of cooperation.

(5) Future research should attempt to incorporate the suite of new technologies available for assessing and manipulating cooperative behaviours wherever possible, since, by borrowing techniques and tools from other disciplines to probe helping behaviour, we may gain a deeper understanding of how cooperative actions evolved in *N. pulcher* as well as in other cooperative organisms.

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