Introduction

Cooperative breeding – characterized by the joint care of young produced primarily by dominant group members – is widespread in animals, including invertebrates, birds, and mammals (Brown 1987; Stacey and Koenig 1990; Solomon and French 1997; Bourke 2011). Unequal partitioning of reproduction or “reproductive skew” is paramount for this type of social system (Hager and Jones 2009). Usually, groups form by the extended philopatry of offspring, which causes high degrees of relatedness within groups (Koenig et al. 1992; Bourke 2011). Therefore, kin selection has been considered to be the major explanatory framework for the cooperative behavior of group members having no or a lower share of the group’s reproduction (Hamilton 1964; Griffin and West 2003; Bourke 2011).

The story is quite different in fish, where cooperative breeding has been described in roughly 25 species of cichlids and a few other species (Taborsky 1994). In the cooperatively breeding fish species investigated thus far, relatedness among adult group members on average seems to be low. This makes fish extremely well suited to study the importance of evolutionary mechanisms other than kin selection that can generate advanced sociality.

At first glance, it is puzzling why cooperative breeding is so rare (<0.1% of 32,700 known fish species). Most importantly, the majority of fish species show little or no brood care. Their specialty is rather to produce large offspring numbers – quantity instead of quality – and leave them without any postfertilization care. In fish taxa showing brood care, typically only one parent takes responsibility, often caring for several...
clutches at a time (Breder and Rosen 1966; Blumer 1979, 1982). Such efficiency is possible because young fish are usually not fed by their parents and offspring protection is a sharable benefit. Therefore, the effort required to care for them hardly rises with increasing offspring numbers (Blumer 1979; Sargent and Gross 1986). Consequently, only a relatively small number of fish species have biparental care (Sargent and Gross 1986), an apparent precondition for the evolution of cooperative breeding (Komdeur and Ekman 2010). If the number of biparental species is taken as baseline, the percentage of cooperatively breeding fish species is more comparable to that of mammals and birds (ca. 3.5%, based on estimated number of fish species with biparental care; Blumer 1982; Gross and Sargent 1985). In addition, relatively few social and breeding systems of fishes have been studied, and thus there may be quite a few cooperatively breeding fishes that have not yet been detected.

The greatest number of cooperatively breeding fish species occurs among the cichlids (family Cichlidae) of the East African Rift Valley’s Lake Tanganyika. In this deep and ancient lake, some 70 species of cichlids do not raise their young in the mouth like the majority of African lacustrine cichlids, but instead attach eggs to substrate and care for the brood by biparental guarding (Brichard 1978; Kuwamura 1997; Konings 1998). Often this involves keeping predators at bay by aggressive behavior, providing shelters, for instance by digging out holes under stones or collecting empty gastropod shells, cleaning eggs and larvae, and supplying eggs with oxygen by fanning. About one-third of these biparental “substrate brooders” of Lake Tanganyika breed cooperatively (Taborsky 1994; Heg and Bachar 2006).

The reproductive and social systems of these cooperative cichlids vary substantially. Groups may include different numbers of immatures, for instance, whereas the number of mature subordinate helpers varies within narrower limits (with means usually varying between one and three males and/or females; Heg et al. 2005a; Taborsky 2009). Relatedness among group members varies both between species (very low in Julidochromis ornatus, Awata et al. 2005; rather high in Neolamprologus mult fasciatus, Kohler 1997; Taborsky 2009) and within species (Dierkes et al. 2005), which may have strong and unexpected effects on cooperation among group members (Stiver et al. 2005; Zöttl et al. 2013a). Reproduction may be highly skewed among group members (as described here for Neolamprologus pulcher) or rather balanced (J. ornatus, Awata et al. 2005). Different forms of cooperative breeding and other manifestations of cooperative reproduction in fish, including non-cichlids, have been discussed elsewhere (Taborsky 1994, 2009).

Neolamprologus pulcher as a model

As yet, most information on cooperative breeding in fishes has been collected from one of the Lake Tanganyika substrate brooders, the lamprologine cichlid Neolamprologus pulcher (Wong and Balshine 2011). N. pulcher occurs in rocky habitats around the sublittoral zone of the lake. Originally the fish of northern populations were described as Lamprologus brichardi, whereas the southern populations were described as L. (savoryi) pulcher (Poll 1974). A lake-wide genetic comparison of different populations revealed no clear-cut separation between these two morphs, but rather a gradual clinal variation in which differences increased with the distance between sampled populations. Thus, both morphs are now referred to as N. pulcher (Duffner et al. 2007). Incidentally, pulcher is Latin for “beautiful,” which many view as appropriate name.

Social system

Breeding units or “groups” of N. pulcher usually consist of a dominant pair of breeders and a variable number of subordinate individuals ranging widely in size. In the north of the lake, a few breeder pairs have been found without helpers (~5%), whereas breeding units lacking helpers are extremely rare in southern populations (< 1%; Taborsky and Limberger 1981; Heg et al. 2005b). Hence it seems justified to categorize N. pulcher as an obligatory cooperative breeder. On average, groups include a pair of dominant breeders and between five and six subordinate helpers ≥ 15 mm standard length (SL) (Taborsky and Limberger 1981; Balshine et al.
with increasing age of the latter. That is, the largest and most efficient helpers are usually unrelated to their beneficiaries (Dierkes et al. 2005).

(4) Transactions between breeders and helpers over the amount of cooperative effort that subordinates deliver provide opportunities to understand why subordinates pay to stay in the territory of dominants by helping to raise and protect the latters’ broods (Bergmüller and Taborsky 2005). In this situation, relatedness can even reduce cooperative effort (Zöttl et al. 2013a). Thus, cooperative breeding reflects reciprocal trading of commodities.

(5) One particular ecological factor – predation pressure – is the dominating ecoevolutionary trigger of this social system (Taborsky 1984; Heg et al. 2004a). It explains colonial breeding, extended philopatry, altruistic effort of helpers that pay to stay in a safe territory, strategic growth of helpers, and the degree of reproductive skew within groups.

In addition to these features, *N. pulcher* is exceptionally well suited for observational and experimental studies both under natural and standardized laboratory conditions. One or several territories of natural size can be easily hosted in a moderately sized aquarium; all behaviors can be easily observed and individuals can be tracked around the clock; the behavior in seminatural laboratory settings does not differ in most aspects from behavior shown in the field; the complex behavioral repertoire including roughly 30 agonistic, affiliative, and submissive behaviors exerted among group members can be directly observed, video recorded, and experimentally manipulated; groups can be artificially composed of individuals with different sizes, sexes, behavioral types (“personalities”), and degrees of relatedness and familiarity; individuals respond well to experimental alterations of their ecology, social environment, and behavior; and important ecological parameters, such as predation, habitat structure, food, and shelter can be easily manipulated. Furthermore, the physiological and genetic mechanisms controlling behavior can be experimentally studied, as will be outlined below; the recent assembly of the genome sequence of *N. brichardi/pulcher* further facilitates this endeavor (Brawand et al. 2014).

This combination of unique features is the reason why, arguably, *N. pulcher* is among the best understood cooperative breeders regarding the ultimate and proximate mechanisms responsible for its sociality.
In contrast to most other systems, this largely rests on experimental scrutiny, applied both in the laboratory and field.

**Ecology**

*N. pulcher* settles in diverse habitats ranging from pure rock with few holes and crevices to finely structured habitats consisting mainly of empty gastropod shells and small stone rubble (Taborsky and Limberger 1981). Often, extensive colonies dwell on sand substrate that is interspersed with rocks, where group members dig out the required shelters from underneath stones by removing sand with their mouths (Bruintjes and Taborsky 2011). Territories consist usually of a hemisphere of about 25–50 cm radius around one or several shelters and their main function is to provide protection from predators (Taborsky 1984; Balshine et al. 2001).

Territories contain only little food, and sexually mature group members (≥ 35 mm SL) feed primarily on zooplankton in the water column (Taborsky 1982, Gashagaza 1988; Bruintjes et al. 2010). Only small offspring, from fry stage to about 3 cm SL, feed from the bottom and plankton exclusively inside the defended area. The food consists mainly of crustaceans. The fact that food is acquired predominantly outside the territory means that resources within territories are not highly depreciable. Even though there is some competition for shelter space among subordinate group members (Balshine et al. 2001; Werner et al. 2003), group size is not strongly limited by resource competition among group members. Nonetheless, food abundance significantly affects the behavior of group members, including interactions among each other and the work load they take on (Bruintjes et al. 2010).

**Demography**

For their size, *N. pulcher* are very long-lived. Individuals can live > 4 years in the field, and in the aquarium some fish have exceeded 10 years of age, corresponding to a slow growth rate and a rather low reproductive output (especially without brood care helpers; Taborsky 1982; Skubic et al. 2004). Like most fish taxa, *N. pulcher* exhibits indeterminate growth, that is, individuals do not stop growing when reproductively mature. Size is of paramount importance for dominance rank within groups and for the success of aggressive interactions with members of other groups (Taborsky 1985; Hamilton et al. 2005; Reddon et al. 2011a). Growth depends on social rank, group composition, and probably also on cooperative effort, which is very energy demanding (Taborsky 1984; Grantner and Taborsky 1998; Riebli et al. 2011, 2012).

**Group structure**

Breeder males often defend more than one group – a harem – each consisting of a dominant female breeder and subordinate helpers (Limberger 1983; Desjardins et al. 2008a; Wong et al. 2012). Such polygynous males regularly visit the group territories, which may be up to 7 m apart (Figure 16.1). Females and helpers do not switch between groups in such harems, so “groups” consist of the breeding female, a varying number of helpers and young, and a male breeder that may also be associated with other such groups. Groups are usually aggregated in colonies ranging in size from a few groups up to several hundred (Heg et al. 2008b).

Within groups there is a strict dominance hierarchy, with rank determined by body size, even if such differences are small. A number of aggressive displays, overt attacks including physical contact, and affiliative and submissive behaviors are involved in the establishment and maintenance of dominance relationships among group members (Taborsky 1982, 1984; Hamilton et al. 2005). There are sex-specific differences in aggression of dominant breeders toward subordinate helpers (Mitchell 2009a), but rank among helpers is not sex-specific (Dey et al. 2013), even though sex can affect dominance acquisition among same-size subordinates (Riebli et al. 2012), and growth patterns (Hamilton and Heg 2008).

**Reproduction**

Reproduction is highly skewed within groups, with dominant breeders producing the majority of offspring. Nevertheless, both male and female helpers participate in reproduction to a variable extent (Taborsky 2009).
Mature male helpers try to fertilize eggs by surreptitious sneaking when the dominant territory owners spawn. Mature female helpers can produce independent clutches in a different shelter within the group territory or rarely add eggs to the clutch of a dominant female (<1% of clutches; Heg et al. 2008a). While some helpers of both sexes produce their own offspring in the groups where they help, most are non-breeding helpers. Five experimental laboratory studies and one observational field study have provided percentage data for 403 broods containing 17,535 young (Table 16.1). In all of these studies, one to four mature helpers were present in addition to the dominant breeders, which corresponds to the natural situation. Although results varied among studies, comparison of pooled data indicates no significant sex difference in the proportion of broods involving some reproduction by helpers (19.1% for males vs. 13.8% for females; N = 403 broods, Fisher exact test, P = 0.15), but female helpers produced a significantly higher proportion of young than did male helpers (14.5% for females vs. 4.5% for males of larvae or free-swimming fry; N = 17,535 young, χ² = 220, df = 1, P < 0.0001). Two studies in which male and female helpers were present in equal numbers corroborate these results (Heg et al. 2006, 2008a). In these studies, the proportion of broods in which male helpers produced young was significantly higher than the proportion of broods produced by female helpers (18.4% vs. 7.9% of 114 broods; Fisher exact test; P = 0.03), whereas again the number of offspring...
produced by female helpers exceeded the number of offspring produced by male helpers (5.4% vs. 3.7% of 2,550 young; \( \chi^2 = 8.6, df = 1, P = 0.003 \)).

Due to sperm competition with the male territory owner, male helpers can apparently sire only a small number of young in their territory (mean = 4.8 young/brood), whereas female helpers produce on average 40.5 young/brood if they lay a clutch. If more than one mature male helper is present in a territory, the most dominant male helper sires more young than if he is the only male helper (Heg et al. 2008a; Mitchell et al. 2009a). In addition, male helpers can sire offspring parasitically in neighboring territories as well (Heg et al. 2006). The reproductive success of male helpers apparently depends on the composition of their own group and on reproductive opportunities in their neighborhood.

### Cooperation

Immature and mature helpers of both sexes help in all duties of brood care, territory defense, and maintenance. Tasks are shared unequally, dependent on size, sex, and status of group members, and on current demands (Taborsky and Limberger 1981; Taborsky 1984; Desjardins et al. 2008b, 2008c). If several demands appear concurrently, helpers specialize in territory maintenance, whereas female breeders focus on direct brood care and both breeders engage in defense (Taborsky et al. 1986). Among helpers, large individuals may defend more frequently than smaller ones (Taborsky and Limberger 1981), or they may specialize in digging while smaller helpers defend the breeding shelter against egg predators (Bruintjes and Taborsky 2011).

---

**Table 16.1.** Numbers and proportions of broods completely or partially produced by helpers, and numbers and proportions of offspring (i.e., hatched larvae or free-swimming fry) produced by male and female helpers

<table>
<thead>
<tr>
<th></th>
<th>Male helpers</th>
<th></th>
<th>Female helpers</th>
<th></th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Total</td>
<td>Percent</td>
<td>Number</td>
<td>Total</td>
</tr>
<tr>
<td></td>
<td>assigned</td>
<td>number</td>
<td>assigned</td>
<td>assigned</td>
<td>number</td>
</tr>
<tr>
<td></td>
<td>to helper</td>
<td></td>
<td>to helper</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Broods</td>
<td>6</td>
<td>44</td>
<td>13.6</td>
<td>1</td>
<td>44</td>
</tr>
<tr>
<td>Young</td>
<td>57</td>
<td>1,185</td>
<td>4.8</td>
<td>30</td>
<td>1,185</td>
</tr>
<tr>
<td>Broods</td>
<td>15</td>
<td>70</td>
<td>21.4</td>
<td>8</td>
<td>70</td>
</tr>
<tr>
<td>Young</td>
<td>37</td>
<td>1,365*</td>
<td>2.7</td>
<td>108</td>
<td>1,352*</td>
</tr>
<tr>
<td>Broods</td>
<td>3</td>
<td>19</td>
<td>15.8</td>
<td>0</td>
<td>12*</td>
</tr>
<tr>
<td>Young</td>
<td>30</td>
<td>294</td>
<td>10.2</td>
<td>0</td>
<td>217*</td>
</tr>
<tr>
<td>Broods*</td>
<td>5</td>
<td>10*</td>
<td>50.0</td>
<td>0</td>
<td>12*</td>
</tr>
<tr>
<td>Young</td>
<td>14</td>
<td>191*</td>
<td>7.3</td>
<td>0</td>
<td>217*</td>
</tr>
<tr>
<td>Broods</td>
<td>27</td>
<td>102</td>
<td>26.5</td>
<td>2066</td>
<td>11,051</td>
</tr>
<tr>
<td>Young</td>
<td>25</td>
<td>153</td>
<td>16.3</td>
<td>264</td>
<td>3,392</td>
</tr>
</tbody>
</table>

Bruintjes et al. (2011) studied natural broods in the field, whereas all other studies involved experimentally controlled groups in the laboratory containing one or two reproductively mature male and/or female helpers.

* The number of broods or offspring produced with male helpers present differed slightly from the number of broods or offspring produced with female helpers present.

* Only broods of groups with potentially mature helpers are considered (inferred from size and state of genital papilla; \( N = 7 \) broods with one, 1 with two and 2 with three mature male helpers present; \( N = 7 \) broods with one, 3 with two and 2 with four mature female helpers).
Costs of cooperation

The effort helpers and breeders show in brood care, territory maintenance, and defense is costly with respect to energy, time, and risk. Energy consumption is increased particularly by digging (six-fold increase of routine metabolic rate; Grantner and Taborsky 1998) which is mainly performed by helpers and female breeders. Dominant male breeders, in contrast, usually invest little in territory maintenance, but instead engage in aggressive behaviors, which are energetically less demanding. Regarding direct brood care, energetically demanding fanning behavior is mainly shown by breeder females, whereas cheaper egg cleaning behavior is shared between breeder females and helpers (Taborsky and Grantner 1998; Zöttl et al. 2013c).

The energy budgets of group members are mainly determined by standard metabolism. Social behaviors such as aggression and submission among group members make up the bulk of the behavioral time budgets of both breeders and helpers, with aggression dominating the time and energy budgets of breeders, and submissive behavior those of helpers (Taborsky and Grantner 1998). Among cooperative behaviors, territory maintenance, which Besides digging includes also removal of stones, shells, and particles (“carrying”) as well as substrate cleaning (cleaning walls and ceiling of the breeding shelter), fills a considerable proportion of the behavioral time budget of helpers and female breeders (Taborsky 1982). This brings about high energetic costs, as these behaviors, especially digging and carrying, use much energy. During breeding, digging was found to be responsible for nearly 20% and 25% of behavioral metabolic costs in helpers and female breeders (Taborsky et al. 2007). Helpers of both sexes dig similarly often, but large helpers take a greater share than small ones when challenged by experimental addition of sand (Bruintjes and Taborsky 2008, 2011).

Depending on demand, helpers take over a substantial amount of territory defense against conspecifics and predators (Bruintjes and Taborsky 2008; Heg and Taborsky 2010; Zöttl et al. 2013b). Large, piscivorous predators are attacked most often by male breeders, followed by female breeders and large helpers. Defense against dangerous predators is often shared, and strategic risk sharing among group members is suggested by significant positive correlations between group size and the per capita attack frequencies of breeders and large helpers against experimentally deployed large predators (Heg and Taborsky 2010). Such behavior apparently reduces mortality risk, since members of large groups survived experimental exposure to predation better despite their higher defense effort (Heg et al. 2004a).

Helpers grow more slowly than individuals living outside of reproductive groups (Taborsky 1984). This can be due both to their submissive status in the group and to their cooperative investment in energetically demanding activities. Experimental evidence shows, however, that the speed of growth depends also on strategy: helpers stay small to remain tolerated in a territory while accumulating reserves for boosting growth after they leave the territory in preparation of independent breeding (Taborsky 1984; Heg et al. 2004b).

Benefits of cooperation

The offspring produced in the territory are the primary beneficiaries of cooperative care, as the helpers present in the group substantially raise their survival chances (Brouwer et al. 2005). However, benefits to breeders arise also through enhanced reproduction in the presence of helpers made possible by the reduced energy expenditure of breeders in the presence of helpers (Taborsky 1984). With increasing helper number, for example, female breeders reduce egg size (Taborsky et al. 2007). Apparently, females with many helpers can afford this economy measure of producing smaller young because of the greater protective effect of a larger group, which increases offspring survival.

Helpers benefit from increased survival through the protection they get in the territory, which results from access to safe shelters and the defensive effort of large group members against dangerous predators (Taborsky 1984). This protective function of large group members (including breeders and large helpers) is so important that at least in the best studied population in the south of Lake Tanganyika, there are hardly any individuals...
living on their own (Stiver et al. 2004). Furthermore, helper-sized fish given the choice prefer larger groups (Reddon et al. 2011b), which persist longer (Heg et al. 2005b). Experimental manipulation of predation risk revealed that members of large groups benefit from higher survival (Heg et al. 2004a).

Benefits to helpers also accrue from the possibility of sharing reproduction in a safe territory (Table 16.1). As there are numerous duties when attempting to monopolize a safe place to live, the sharing of these duties can increase efficiency, allowing individuals to save effort without losing the benefits. Furthermore, in *N. pulcher* joint offspring production can affect cooperation. When male helpers in the field sired part of the offspring produced in a territory, they increased their defensive effort against egg predators (Bruintjes et al. 2011).

**Division of labor**

The efficiency of cooperation is strongly determined by the specialization of individuals in different tasks. In *N. pulcher*, indeterminate growth causes group members to differ in size, and consequently dominance status, which correlates with age and is affected by social and environmental conditions (Taborsky 1984; Skubic et al. 2004; Hamilton and Heg 2008). This variation in size provides the basis for temporal behavioral specialization of group members in divergent cooperative tasks (temporal polyethism). Field and laboratory experiments showed that the tasks breeders and helpers of different sizes perform depend on the intrusion of competitors and the type of predators, and on the need for direct brood care and sand removal (Taborsky et al. 1986; Bruintjes and Taborsky 2011; Zöttl et al. 2013b). Female breeders generally seem to prioritize defense of the territory regardless of the type of intruder, whereas helpers and male breeders distinguish more strongly between different types of threat (Desjardins et al. 2008b).

When large or medium-sized *L. elongatus* predators were introduced into large cages containing parts of *N. pulcher* colonies in their natural environment, 30% of aggressive displays and attacks were performed by large helpers, whereas female breeders contributed 26% and male breeders nearly 44% of aggressive acts. In contrast, the share of medium sized helpers was only 0.3%, while small helpers did not attack these predators at all (Heg and Taborsky 2010).

**Load lightening and compensation**

When different group members cooperate in the performance of duties, loads may be lightened for each participant. However, selection should favor individuals that hold back investment if others will compensate (Houston et al. 2005; Johnstone et al. 2014). This problem is particularly relevant if several individuals share the effort, as in cooperatively breeding groups (Johnstone 2011).

In *N. pulcher*, the cooperative effort of helpers in brood care and territory maintenance reduces the load to female breeders, which can in turn increase their reproductive rate (Taborsky 1984; Heg 2008). Females with helpers are apparently less stressed than those without helpers, as indicated by reduced egg cortisol levels (Mileva et al. 2011). In addition, females lay smaller eggs when receiving more help, as mentioned earlier. Experiments reveal that load-lightening effects and negotiation over brood care determine the investment decisions of both breeders and helpers. When helpers were experimentally prevented from sharing in direct brood care, the female breeder compensated for the lack of help by increasing her egg cleaning effort and the removal of sand from the breeding shelter (Zöttl et al. 2013c). Nevertheless, the total amount of brood care and breeding shelter maintenance was lower when the female breeder was not supported by her helper. This shows that the idleness of brood care helpers is only partially compensated by the dominant, as predicted by theoretical models (McNamara et al. 2003). After the experimental prevention of help, *N. pulcher* helpers increased their effort in these duties, thereby compensating for withheld cooperative investment in the preceding time period.

In another experiment, the effect of the helpers’ compensation of withheld cooperation on their subsequent investment in brood care was tested by either allowing the dominant breeders to interact with the behaviorally manipulated helper or not (Schreier
Compensatory help after a period of withheld cooperation was only found when direct interactions between dominant breeders and subordinate helpers were allowed, highlighting the importance of negotiations for the latters’ propensity to fulfill costly altruistic tasks. Compensatory responses of helpers to prevented help, but without manipulation of the dominants’ behavior, were also revealed by other laboratory and field experiments (Bergmüller and Taborsky 2005; Fischer et al. 2014).

**Evolutionary mechanisms underlying cooperative breeding**

Cooperative breeding has two critical components: the delayed (or withheld) dispersal of subordinate group members, and their cooperative care of young that are not their own (Komdeur 2006). These two components of sociality, reflecting decisions of group membership and cooperation, are subject to different ecological and social conditions although they likely evolve in concert (Aktipis 2004; Hamilton and Taborsky 2005a; Hochberg et al. 2008).

**Why delay dispersal?**

Several hypotheses attempt to explain delayed dispersal of subordinates focusing either on the costs of dispersing or the benefits of staying (Emlen 1982; Koenig et al. 1992; Stacey and Ligon 1991). In *N. pulcher*, there are clear benefits of philopatry. Individuals in the size range of helpers gain a substantial survival benefit from the defensive efforts of large group members, particularly the dominant breeders (Taborsky 1984). Helpers experimentally separated from their home territory are not accepted in other groups (Taborsky and Limberger 1981), and even if helpers can switch into a different group, this occurs only rarely (~3.5% of helpers in a sample of 205 genotyped individuals from 31 groups; Dierkes et al. 2005). In southern populations of *N. pulcher*, almost all individuals are members of a group that includes a breeding pair (Heg et al. 2005a, 2005b). In contrast, in the north of Lake Tanganyika the majority of sexually mature fish live in permanent, nonreproductive aggregations that provide protection and serve as a reservoir of breeders ready to fill vacancies (Taborsky and Limberger 1981).

In addition to affecting survival, prolonged residence in the natal territory determines the opportunity to reproduce, even if reproductive skew is high (Table 16.1). Staying home means a safer but lower reproductive output than leaving and breeding independently; it also provides a chance to inherit breeding status if the same-sex breeder disappears (Balshine-Earn et al. 1998; Stiver et al. 2006). Such territory inheritance is sex-specific, with female helpers inheriting the territory from their mother or sister in 19% of cases (this was more likely in large than in small groups), whereas male helpers inherited their parental territory only in 3% of the surveyed groups (these are minimum estimates; Dierkes et al. 2005).

Males are less likely to inherit and more likely to disperse. In a northern population, nonbreeding aggregations consisted of twice as many males than females, whereas within breeding groups the sex ratio of similar sized individuals was exactly opposite (Taborsky 1984, 1985). Accordingly, in a southern population dispersal distances of males were greater than those of females (Stiver et al. 2007).

When one or both breeders were experimentally removed from groups containing large, sexually mature helpers, northern population helpers failed to take over the vacant dominant position, whereas in a southern population the largest helper took over in 7 of 18 replicates (Taborsky and Limberger 1981; Balshine-Earn et al. 1998). Parallel experiments in this latter population showed that larger female helpers were more likely to take over a vacant dominant breeder position than were larger male helpers (Stiver et al. 2006), corroborating the higher territory inheritance probability of female than male helpers.

The striking difference in territory inheritance patterns between the north and south of Lake Tanganyika is probably due to different population structure. As outlined earlier, in the north most sexually mature individuals live in stable aggregations located next to breeding territories. In contrast, in the south there are no aggregations of nonreproductives, and only about 5% of individuals do not belong to a breeding group.
Hence, takeovers there often involve large helpers or breeders of neighboring groups (Stiver et al. 2006). The resulting mean relatedness between social mates does not differ from a pattern generated by random pair formation, which suggests neither avoidance nor preference of pairing with relatives. Disregard of existing relatedness was suggested also by gonadal investment of subordinates living in social groups, as this was not correlated with their relatedness to the opposite-sex dominant breeder in the group (Stiver et al. 2008).

Dispersal decisions of helpers depend primarily on the risk of predation, but they are also influenced by the availability of vacant breeding positions and the quality of the home territory. In a field study of a population dwelling on a mixed rock/sand habitat, experimental provisioning of territories at the edge of a colony did not cause subordinate group members to disperse and breed independently, but territories provided at similar distances within the colony were readily inspected and taken over both by *N. pulcher* and the closely related, syntopic cooperative breeder *N. savoryi* (Heg et al. 2008b). When in contrast the quality of the home territory was diminished by experimentally reducing the number of shelters, helper numbers in such territories declined (Balshine et al. 2001). Laboratory experiments revealed that breeding habitat availability significantly affects dispersal decisions (Bergmüller et al. 2005a), but habitat saturation is not a prerequisite of delayed dispersal: depending on body size, subordinate individuals often prefer to stay with dominants, even if they are unrelated and alternative options to breed independently are available (Taborsky 1985, Heg et al. 2011). When joining an unfamiliar group, helpers prefer to join large over small groups and groups containing large, more dominant individuals, in spite of incurring greater aggression and a reduced chance of inheriting the territory (Jordan et al. 2010; Reddon et al. 2011b). This again suggests that the primary function of group membership is protection against predation.

Experimental manipulation of predation risk in the field (Figure 16.2) showed that helpers adjust their behavior, spacing pattern, and dispersal propensity to the level of predation risk (Heg et al. 2004a; Heg and Taborsky 2010). Even when dispersal vacancies were available to helpers, they dispersed principally only when large predators were excluded from the

Figure 16.2. Results from a field experiment in which the predation risk was experimentally varied by adding either no (control), a medium, or a large predator (*Lepidiolamprologus elongatus*) to an 8 m³ cage containing part of a natural *N. pulcher* colony (left panel; 21 cages (replicates) were used in total). Middle panel: Digging effort of small, medium and large helpers in the three experimental situations. In the large predator treatment, large helpers in particular engaged a lot in digging out a shelter that was experimentally covered with sand. Depicted are means ± standard error (S.E.) and sample sizes (*N* groups). Right panel: Number of experimental cages in which helpers dispersed (black) of 7 cages each per treatment. After Heg et al. (2004a), Heg and Taborsky (2010).
area (Figure 16.2). This seems to reflect an adaptive response to current predation risk, as in the presence of large predators, membership in large groups significantly increased survival. Hence, the decision to delay dispersal is apparently triggered by an ecological constraint – predation risk – that contrasts with constraints observed in many other cooperative breeders, where dispersal is limited primarily by the availability of territories or breeding habitat (Emlen 1982; Koenig et al. 1992). Similarly, in Siberian jays (*Perisoreus infaustus*), predation seems to select for philopatry due to effective antipredator behavior of parents, but in the jays, where subordinates do not help, protection is typically withheld from unrelated group members (Griesser et al. 2006; Chapter 1).

Reproductively mature helpers survey their environment not only for local predation risk, but also for suitable breeding habitat and for groups they may join. When helpers were experimentally provided with dispersal opportunities that either did or did not contain breeding substrate, they only dispersed when breeding opportunities were supplied (Bergmüller et al. 2005a). This coincided with a significant reduction of submissive and helping behaviors while still in their home group and with a significant increase in body mass. Thus, helpers strategically reduce effort at home to accumulate reserves for their own reproduction once they have decided to leave and breed independently. These experimental results were corroborated by field data showing that helpers reduced cooperative antipredator defense in their home territories shortly before they dispersed, while helpers inheriting their natal territories did not do so (Zöttl et al. 2013d).

In the field, helpers spend about 5% of their time visiting other groups that can serve as a refuge if conditions turn unfavorable in their home territories (Bergmüller et al. 2005b). Experimentally increasing the perceived risk in the home territory with a fish predator dummy resulted in helpers taking shelter in one of the previously visited territories and even in some cases dispersing to that territory. Such visits to other groups occur more often when helpers are part of a long queue in their home territory, suggesting that helpers may use these visits not only as an insurance strategy, but also to explore future reproductive opportunities in neighboring groups.

### Why help?

Four evolutionary mechanisms may select for the apparently altruistic behavior of helpers (Lehmann and Keller 2006): (1) reciprocity (e.g., commodity trading among group members), (2) direct selfish benefits, (3) kin selection, and (4) genetic correlation between altruism and identifier genes ("greenbeard genes"). In *N. pulcher*, the first three of these mechanisms are apparently present, but it seems that reciprocity is most important for the cooperative behavior of large, sexually mature helpers. There is no evidence for green-beard genes in this species, hence this mechanism will not be considered.

### Reciprocity

Subordinate group members can entail costs to dominants because of resource competition. This may be compensated by cooperative behavior of subordinates, implying that “helping-at-the-nest” serves as “payment of rent” (Gaston 1978; Kokko et al. 2002). In *N. pulcher*, helpers have been shown to pay for being allowed to stay (Taborsky 1985), which provides them with resource access (safe shelters; Heg et al. 2008b), protection due to group antipredator defense (Taborsky 1984), and opportunities to reproduce (Table 16.1). The costs helpers can incur to dominants include competition for shelters, behavioral expenditure diminishing growth and reproductive competition (Dierkes et al. 1999; Balshine et al. 2001; Heg and Hamilton 2008; Heg et al. 2008a; Mitchell et al. 2009a, b). The latter is indicated also by a positive correlation of the testis mass of male breeders with the number of male helpers (Fitzpatrick et al. 2006).

If accepting subordinates is costly to dominants, the latter will be selected to demand compensation (Kokko et al. 2002; Hamilton and Taborsky 2005b). The ensuing pay-to-stay mechanism involves four components: (1) a latent threat to idle subordinates (Cant 2011), (2) an increase in cooperation by subordinates in response to threats or sanctions (Raihani et al. 2012), (3) a demand-driven propensity for dominants to exert...
pressure on subordinates to make themselves useful (Taborsky 1985), and (4) a scaling of the response of subordinates to the demands of dominants based on the subordinates’ outside options (Bergmüller et al. 2005a).

These components have been experimentally identified in the interactions among group members. Dominants regularly exert aggression toward subordinate group members and may evict subordinates from their territory, thereby posing a latent threat (Taborsky 1985; Dierkes et al. 1999). In particular, dominants may punish subordinates for being idle when help is needed, as revealed by manipulation of subordinates’ behavior in the field (Fischer et al. 2014). Subordinates increase help after being experimentally prevented from helping, which may appease dominants preemptively (Bergmüller and Taborsky 2005) or constitute a response to increased aggression of dominants (Fischer et al. 2014).

Dominants expel subordinates from their territories in the absence of predators and competitors, that is, when they are not needed, and readily reaccept them when threat of competition or predation is experimentally increased (Taborsky 1985). Increased demand by territory intrusion pressure may lead to the acceptance of unrelated and unfamiliar helpers (Zöttl et al. 2013b). Subordinates adjust their effort when their outside options are manipulated. If they are provided with an opportunity to disperse and breed independently, in a safe environment, they reduce the help they provide to dominant breeders (Bergmüller et al. 2005a). In contrast, if the benefits of group membership are experimentally increased by raising predation risk, helpers increase their effort with each aggressive act received from dominants (Heg and Taborsky 2010). Although helpers reduce their effort prior to dispersing to a breeding position elsewhere, they maintain high investment when staying to take over their natal territory (Zöttl et al. 2013d).

Why do we consider this somewhat enforced trading of commodities an example of “reciprocity” rather than “coercion”? Both parties have alternative options, so when the costs of cooperation reach an unacceptable level for one of them, they can end the relationship; dominants by expelling the subordinate, and helpers by leaving the group. Cooperation cannot be completely enforced by dominants; it can only be demanded up to a point where benefits to be gained by outside options of the subordinate partner exceed the benefits it can obtain in the group (Cant and Johnstone 2009). By attacking helpers that do not fulfill the demand, dominants can modify the cooperative propensity of subordinates through imposing costs of idleness, but they cannot make subordinates help if they do not provide benefits in return. Hence, the concept of “reciprocal trading” adequately describes pay-to-stay scenarios such as observed in *N. pulcher*. It will be a worthwhile challenge for future studies to unravel evolutionarily stable negotiation rules of reciprocating group members.

**Direct selfish benefits**

Behaviors that benefit others may also provide selfish benefits to the actor. For instance, if a helper removes sand from the breeding shelter, this benefits the offspring of dominants growing up in the same cavern, but the helper may also derive benefits from hiding in the enlarged shelter when threatened by a predator. Hence, the benefits provided by helpers to dominant breeders may be a side effect of selfish behavior. Mutual benefits to group members also accrue to helpers by positive effects on group size, given that large group size enhances survival and is thus beneficial, an effect that has been referred to as “group augmentation benefits” (Kokko et al. 2001; Kingma et al. 2014). If group augmentation benefits select for helping behavior, two conditions must be fulfilled: fitness benefits of helpers must increase with group size, and helping must drive larger group size.

Both conditions are met in *N. pulcher*. In nature, helpers survive better in large than in small groups (Heg et al. 2004a, 2005a). Benefits of producing additional group members may also result when helpers take over their natal territory, if these group members will then help to raise the offspring of the former helper (long-term group augmentation benefits, or “delayed reciprocity;” Ligon and Ligon 1978; Wiley and Rabenold 1984; Kingma et al. 2014). In *N. pulcher*, female helpers frequently (~20%) inherit territories (Dierkes 2005), creating opportunities for delayed reciprocity. Delayed...
benefits of group augmentation may also accrue if helpers disperse jointly with the recruits they have helped to produce, but we have no evidence for joint dispersal of helpers and recruits in *N. pulcher*.

Subordinates increase the production of dominants’ offspring, and hence increase group size by helping, in two ways: they lighten the workload of female breeders who thereby produce larger clutches, and they increase the survival of young (Taborsky 1984; Brouwer et al. 2005). Hence, both conditions for selection based on group augmentation benefits are fulfilled, suggesting that this mechanism plays a role in driving helping decisions.

**Kin selection**

Above-average relatedness within groups is a standard condition in cooperative breeders because group formation is typically based on delayed dispersal (Koenig et al. 1992). Kin selection will take effect if subordinates and dominants are related, and if subordinates raise the production of dominants’ offspring. The latter condition applies to *N. pulcher* as outlined earlier, whereas the first condition is only partly met.

*N. pulcher* groups consist of a mixture of related and unrelated individuals. On the one hand, above average relatedness is caused by the delayed dispersal of young, which is responsible for significant age-assortative genetic relatedness among subordinates within groups (age cohorts, Dierkes et al. 2005; Figure 16.3a). On the other hand, relatedness between subordinates and dominants is diminished by the fact that helpers stay in the territory after one or both dominant breeders are replaced by unrelated immigrants (Taborsky and Limberger 1981; Balshine-Earn et al. 1998). This happens regularly, and as a result the relatedness between sexually mature helpers and dominant male breeders is not greater than the population mean. Mean relatedness between female breeders and their sexually mature helpers is also low, but significantly higher than the average relatedness level in the population (Dierkes et al. 2005; Figure 16.3b). This sex difference in relatedness of helpers is mainly caused by sex-specific replacement rates, with male rates exceeding those of females, combined with a greater propensity of males to disperse, resulting in about 20% of groups involving matrilines compared to virtually no groups involving patrilines. The greater

---

**Figure 16.3.** (a) Genetic relatedness between helpers of different size (i.e., age) within *N. pulcher* groups measured in the field (*N* = 3,288 helpers). The slopes of the relatedness landscape reveal that average relatedness declines with increasing age, and that helpers within age cohorts are much more closely related than those between cohorts. (b) Within-group relatedness of helpers to male and female breeders. The average degree of relatedness to breeders declines with size (i.e., age) of the helpers due to the natural turnover rate of breeders, and the decline in relatedness to male breeders is much greater than that to female breeders due the higher turnover rate of male territory owners. From Dierkes et al. (2005).
dispersal distances of males in comparison to females (Stiver et al. 2007) may also affect this sex-specific relatedness pattern.

In addition, relatedness between breeders of both sexes and helpers is reduced by the production of extra-pair young. Although the numbers of extra-pair young produced by helpers of both sexes is generally low (Table 16.1), unrelated neighboring males also fertilize some of the eggs produced in a territory (Stiver et al. 2009; Bruinjes et al. 2011), further reducing relatedness within groups.

There is nonetheless scope for kin selection being important via relatedness to the female breeder (Figure 16.3b). In addition, _N. pulcher_ of helper size have been shown to recognize kin, apparently by phenotype matching (Le Vin et al. 2010). These conditions may select for altruistic helping especially in small, young helpers (Bruinjes and Taborsky 2011), as relatedness declines with helper size. The asymmetrical relatedness between helpers and male vs. female breeders predicts that helping effort should differ depending on the sexes involved. This has been corroborated by field data showing that helpers related to female breeders invest more in cooperative defense than helpers unrelated to female breeders, whereas helpers unrelated to the male breeder showed higher defense effort than related ones (Stiver et al. 2005). The first result supports an effect of kin selection, whereas the latter result suggests the importance of paying rent for being allowed to stay in the territory.

The relative importance of kin selection and reciprocity can be determined by experimental manipulation of relatedness between helpers and beneficiaries. _N. pulcher_ is one of the few systems were this can be done because of the natural dynamics of group formation. As a result, groups can be experimentally assembled of related or unrelated members, and we can expect that members of such groups will respond to the variation of relatedness in a meaningful way if relatedness is important for the selection of helping behavior. This approach has been used by two experimental laboratory studies. In the first, helping levels were compared between groups made up of helpers related to both breeders and groups with helpers unrelated to both breeders. The work effort of helpers in the unrelated treatment exceeded that of helpers in the related treatment by roughly ten-fold (Stiver et al. 2005).

In the second study, female helpers were either daughters or sisters, or unrelated to the female breeder, while they were always unrelated to the male breeder. This study focused on direct brood care (egg cleaning and fanning), because these behaviors clearly have costs (Taborsky and Grantner 1998) but do not entail direct fitness benefits and thus are unambiguously altruistic. Again, unrelated helpers showed more care for dominant females’ broods than did related helpers (Figure 16.4). In addition, they also invested more effort in digging out the breeding shelter, which is energetically demanding (Grantner and Taborsky 1998). When egg cannibalism of helpers was experimentally simulated, unrelated helpers responded with increased alloparental care, whereas related ones did not (Zöttl et al. 2013a).

Hence, both studies confirm that helping behavior is better explained by reciprocity (pay-to-stay) than by indirect, kin-selected fitness benefits. Furthermore, experiments showed that individuals given the choice to settle with related or unrelated individuals avoid the former (Heg et al. 2011), which indicates that subordinates may even prefer reciprocal to kin-based relationships in their group.

### Helping personality

Consistent behavioral variation among individuals of a group or population, known as “animal personalities” (Reale et al. 2010), is particularly interesting in species with long-term, close social relationships such as cooperative breeders because they may facilitate social coexistence and enhance potential synergies of cooperation (Bergmüller and Taborsky 2010). Group members of _N. pulcher_ differ consistently in their propensity to perform certain tasks such as territory maintenance, defense, and exploration (Bergmüller and Taborsky 2007; Schürch and Heg 2010a; Le Vin et al. 2011). Consistent behavioral variation in helpers implies strategic specialization in different life history stages, and an efficient distribution of tasks.
among group members due to the specialized functions fulfilled by different individuals (Bergmüller and Taborsky 2007; Bruinjes and Taborsky 2011). The positive correlation between the propensities to dig and to defend the territory, particularly in immature helpers, suggests the existence of more helpful and more selfish phenotypes (Schürch and Heg 2010a; Le Vin et al. 2011). After sexual maturation, the relationship between helping behavior and different behavioral propensities such as exploration, boldness, and aggression varies between the sexes. In adult female helpers, they are all part of the same behavioral syndrome, whereas in adult male helpers this does not seem to apply; instead, their helping behavior is negatively correlated with the propensity to disperse (Schürch and Heg 2010a).

The behavioral type of individuals can affect dominance relationships and growth (Riebli et al. 2011). The effect of behavioral idiosyncrasies on the likelihood of obtaining dominance and a high quality territory in groups of four similar-sized conspecifics was small, whereas effects on growth and the accumulation of reserves were more pronounced, with low-aggression individuals typically growing faster than more aggressive ones (Riebli et al. 2012). These studies reveal an important modulating effect of the social environment on the link between behavioral types and life history decisions, in accordance with the social niche hypothesis of animal personality evolution (Bergmüller and Taborsky 2010). This hypothesis proposes that adaptive adjustment to the social environment may generate behavioral consistency, which in turn can have long-lasting effects by diminishing conflict among conspecifics due to reduction of niche overlap between individuals sharing resources. In N. pulcher, the behavioral type of individuals during early development were indeed shown to have long-lasting effects, including effects on reproductive decisions and the propensity to accept subordinates in their group after attaining a dominant breeder position (Schürch and Heg 2010b). Furthermore, behavioral types of adults influence which type of subordinates dominants accept in their group, with bold and shy male breeders preferably accepting helpers of similar type (Schürch et al. 2010).

These results reveal that the behavioral type of individuals partly explains interaction patterns within groups and also group composition. Importantly, behavioral types in N. pulcher are consistent over a lifetime and heritable (Chervet et al. 2011), suggesting that they are subject to natural selection. Indeed, in N. pulcher, personality type explains the propensity to invest in helping behavior even better than does relatedness (Le Vin et al. 2011).
Developmental and maternal effects on helping behavior

Social experience may strongly affect behavioral decisions (Rutte et al. 2006; Champagne 2010). This is of particular importance in group-living species because early social experience can be varied and complex, and potential effects on social behavior may influence social relationships of the individual and the group.

“Social competence” refers to the ability of individuals to respond optimally to available social information, which is a skill largely obtained by prior social experience (Taborsky and Oliveira 2012). In N. pulcher, the social experience made during the first 60 days after hatching affects behavioral decisions and social competence throughout life. For example, in experiments using a split brood design, young growing up with adults (dominant breeders with or without helpers) interact more aggressively and submissively among each other than their siblings growing up without adults (Arnold and Taborsky 2010).

Higher social competence apparently results in more efficient conflict resolution (Hick et al. 2014). When two fish of similar size were made owners of the same shelter and competed for it 6 to 12 months after their experimentally controlled rearing conditions, both winners and losers of this contest behaved more adequately (showing more open aggression and submission, respectively), when they had been raised with adults during their first 60 days after hatching than when they had been raised among same-aged peers only (Taborsky et al. 2012). Such competence allowed the socially experienced losers to be tolerated by winners closer to the desired shelter, and later in life to be admitted as subordinates in the territory of unfamiliar and unrelated breeders.

Analysis of gene expression profiles revealed that genes coding for the neuropeptide CRF (corticotrophine-releasing factor) and the steroid hormone receptor GR1 were differently expressed in the fish raised in divergent social environments. Thus, the brains of the fish are affected by their early social experience, which irreversibly alters the expression of these two key gene products regulating the stress response (Taborsky et al. 2013).

The social environment also influences maternal effects that are apparently strategic, with females reducing egg size when assisted by greater numbers of helpers (Taborsky et al. 2007). This corresponds to the productivity increase of females with helpers, which are able to lay larger clutches (Taborsky 1984).

Physiological control of social behavior

One of the key questions regarding the proximate mechanisms of altruistic behavior concerns the hormonal and endocrine mechanisms underlying the motivation and execution of alloparental care (Ziegler 2000). In N. pulcher, the cleaning of eggs by nibbling off microorganisms from their surface is a delicate behavior that can easily change into egg eating. The helpers’ decision to clean instead of cannibalize eggs depends on their body size or age, dominance status, and previous experience with eggs (Siemens 1990). As brood care behavior in vertebrates, including teleost fishes, is often regulated by prolactin (Whittington and Wilson 2013), this protein is a likely candidate for the proximate causation of direct brood care behavior, which in addition to cleaning involves also fanning of eggs in N. pulcher. However, neither the measurement of the expression of prolactin mRNA in the pituitary gland of breeders and helpers, nor the intraperitoneal application of ovine prolactin, have indicated that this hormone is involved in the regulation of direct egg care in this species (Bender et al. 2008a). Brood-caring adult females even showed lower gene expression levels of prolactin than adult female nonbreeders. Other candidate neuropeptides for the regulation of altruistic brood care behavior include the nonapeptides isotocin, the teleost homologue to mammalian oxytocin, and the close relative vasotocin, the teleost equivalent to mammalian vasopressin. These trigger a host of social behaviors including cooperation and brood care (Donaldson and Young 2008; Godwin and Thompson 2012; O’Connell et al. 2012). Studies of the potential effects of these neuropeptides on direct brood care and other helping behaviors in N. pulcher are currently lacking, but isotocin and arginine vasotocin affect social sensitivity and preference as well as dominance.
Steroid hormones can also trigger brood care, especially in males (Knapp et al. 1999). In *N. pulcher*, however, brood care does not seem to relate to steroid hormone excretion levels (Bender et al. 2008b). Interestingly, cortisol levels are reduced in helpers showing much submissive behavior, suggesting that helpers can reduce social stress by appeasing dominant breeders (Bender et al. 2006). Testosterone and 11-ketotestosterone levels were also reduced in helpers showing high levels of submissive behavior. This connection between signals of submission and the reproductive status of subordinate male helpers indicates that submissive behavior may honestly reveal to male breeders a low reproductive potential of highly submissive male helpers.

Steroidal androgens are important mediators of social behavior, especially aggression and male reproductive behaviors (Ros et al. 2004). In *N. pulcher*, excreted androgen levels were similar between male breeders and male helpers (Oliveira et al. 2003; Bender et al. 2006), whereas plasma 11-ketotestosterone was higher in male breeders than male helpers when groups were sampled in the field (Desjardins et al. 2008b). Females, in contrast, showed the highest testosterone values of all group members, which were positively correlated with their territory maintenance and defense behaviors. In general, dominance interactions in *N. pulcher* seem to be mediated mainly by testosterone in females and 11-ketotestosterone in males (Hirschenhauser et al. 2004, 2008; Aubin-Horth et al. 2007; Taves et al. 2009).

**Conclusions**

*Neolamprologus pulcher* is an ideal model for the study of ultimate and proximate mechanisms underlying cooperative breeding due to a combination of complex social traits and unique possibilities for experimentation. These characteristics have allowed us to determine and test experimentally the factors important to cooperative breeding in this species. These include an important role of predation in dispersal decisions, the reciprocal trading of commodities between dominants and subordinates, a relatively minor influence of relatedness on helping decisions compared to reciprocity-based altruism, and a striking efficiency of task sharing based on behavioral specialization of group members. The combination of these traits is evident across populations of *N. pulcher*, an ecologically highly successful species that has colonized Lake Tanganyika all along its shores. Their social dynamics allow the application of experimental approaches both to the fitness-relevant costs and benefits of behavioral and life history decisions and to the proximate mechanisms controlling these decisions at genetic and physiological levels, providing many promising future research avenues.

**Acknowledgments**

I am very grateful to Janis Dickinson, Joachim Frommen, Arne Jungwirth, Walt Koenig, and Barbara Taborsky for constructive criticism and help with the manuscript, and to the Swiss National Science Foundation for financial support (grants 310030B 138660 and 31003A 156152).

**REFERENCES**


Taborsky, B., Tschirren, L., Meunier, C., and Aubin-Horth, N. (2013). Stable reprogramming of brain transcription profiles...


