



Male Norway rats cooperate according to direct but not generalized reciprocity rules

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ARTICLE INFO

Article history:

Received 10 September 2018
Initial acceptance 15 November 2018
Final acceptance 22 February 2019
Available online 27 April 2019
MS. number: 18-00651R

Keywords:

altruism
cooperation
generosity
reciprocity
sex differences

Reciprocal cooperation may evolve if the costs of help are reliably compensated for by delayed returns provided in future interactions. The associated probabilities and cost–benefit ratios may vary systematically between the sexes, which often display different dispersal strategies and interaction patterns. Whereas female Norway rats, *Rattus norvegicus*, are known to apply direct and generalized decision rules of reciprocal cooperation, the rules according to which males reciprocate favours are less well understood. Therefore, we investigated the cooperation propensity of male wild-type Norway rats. Male test rats experienced cooperating partners that provided food to them, or defecting partners that refused to provide help. Afterwards, test rats could donate food to previously experienced or unknown partners, resembling direct and generalized reciprocity paradigms, respectively. Male rats cooperated according to direct reciprocity, suggesting that this decision rule is similarly important for both sexes. However, whereas females additionally help according to generalized reciprocity, males did not apply this rule. These results suggest a sex difference in reciprocal decision rules, highlighting the potential importance of different interaction patterns and cost–benefit ratios between the sexes.

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Evolutionary theory predicts individuals will behave in their own interest (Darwin, 1859). Nevertheless, in many species individuals cooperate by providing costly help to others (Dugatkin, 2002; Krause & Ruxton, 2002; Taborsky, Frommen, & Riehl, 2016). The evolution of such cooperation depends on its costs and benefits (reviewed in: Lehmann & Keller, 2006; Nowak, 2006). These costs and benefits, however, may vary between individuals based on intrinsic asymmetries, for instance in need or strength (Phillips, 2017). Furthermore, cost–benefit ratios may differ between the sexes. In fact, sexual selection theory predicts significant sex differences in cooperation (Darwin, 1859). While males in a group often compete with each other for access to females, females often benefit from one another, for instance in the context of reproduction (Weidt, Lindholm, & König, 2014). Therefore, females may be more cooperative in such systems. In primates, for instance, intrasexual competition has been proposed to explain social systems in which males are generally less cooperative than females (Kappeler & van Schaik, 2002; Wrangham, 1979).

Nevertheless, in many species males regularly cooperate with each other, even in the context of reproduction (Díaz-Muñoz, DuVal, Krakauer, & Lacey, 2014; Taborsky, 1994). For instance, male lions, *Panthera leo*, and spider monkeys, *Ateles geoffroyi yucatanensis*, support each other during raids and fights (Aureli, Schaffner, Verpooten, Slater, & Ramos-Fernandez, 2006; Grinnell, Packer, & Pusey, 1995), long-tailed manakin, *Chiroxiphia linearis*, males and male rivals in some fish species court together (McDonald, 1989; Taborsky, 1994), male subordinates of cooperatively breeding birds and fishes help to raise the offspring of others (Reyer, 1984; Taborsky, 2016), and male fiddler crabs, *Uca mjoebergi*, and cichlid fish, *Astatotilapia burtoni*, help to defend their neighbour's territory (Backwell & Jennions, 2004; Weitekamp & Hofmann, 2017). Although these males at the same time compete for females or resources, the costs of cooperation may be compensated for by indirect fitness benefits via relatedness (Hamilton, 1964; Hatchwell, Gullett, & Adams, 2014), immediate direct fitness benefits via mutualism (Clutton-Brock, 2002; Kingma, Santema, Taborsky, & Komdeur, 2014), delayed fitness benefits by reciprocity (Quinones, van Doorn, Pen, Weissing, & Taborsky, 2016; Trivers, 1971), or cooperation may be enforced by the beneficiaries' manipulation (Hager & Jones, 2009; Ratnieks & Wenseleers, 2008).

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The cost–benefit ratio of cooperation is a crucial factor in the evolutionary emergence of decision rules underlying cooperative behaviour (Barta, McNamara, Huszár, & Taborsky, 2011; Rankin & Taborsky, 2009). This is particularly important when help is reciprocally exchanged among social partners, where decisions to help depend not only on features of a partner, such as relatedness, condition and relative rank, but also on previously received cooperative behaviour. Reciprocal exchange of help can establish stable cooperation between kin and nonkin, if costs of help are predictably compensated for by benefits derived from the receipt of help in the future (Axelrod & Hamilton, 1981; Schweinfurth & Taborsky, 2018a). This can in theory occur by three simple decision rules. (1) Direct reciprocity implies that individuals help those that have helped them before (Trivers, 1971). (2) Indirect reciprocity means that individuals help social partners that were helpful towards others before, which demands availability of public information (Alexander, 1987). (3) Generalized reciprocity instead is based on an increased motivation to help others due to help experienced by anyone (Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005).

Probably one of the best investigated model organisms for reciprocal cooperation is the Norway rat, *Rattus norvegicus* (reviewed in Schweinfurth, in press). Thus far, however, most studies have been conducted on female rats. Females have been repeatedly shown to cooperate according to both direct and generalized reciprocity rules in the same cooperative task as used in this study (Dolivo & Taborsky, 2015a; Rutte & Taborsky, 2007, 2008; Schweinfurth, Stieger, & Taborsky, 2017; Schweinfurth & Taborsky, 2016, 2017, 2018b), and they have been shown to cooperate reciprocally also in tasks involving other behaviours such as allogrooming (Schweinfurth, Stieger, et al., 2017; Schweinfurth & Taborsky, 2018b; Stieger, Schweinfurth, & Taborsky, 2017; Yee, Cavigelli, Delgado, & McClintock, 2008). Little is known, however, about the reciprocal decision rules male rats may apply.

On the one hand, reciprocity might be less important for male than female rats because their social lives differ considerably (reviewed in: Barnett, 1963; Calhoun, 1979; Telle, 1966). For example, males show a strong social hierarchy based on fighting ability, whereas females form less stable and more shallow hierarchies (Adams & Boice, 1983; Blanchard, Flannelly, & Blanchard, 1988). Colonies of rats can contain over 200 individuals, and sex ratios are female biased, which results in fewer male–male than female–female interactions (Davis, 1953). Further, males are less tolerant when feeding next to same-sex partners than females (Calhoun, 1979).

On the other hand, reciprocity might be similarly important for both sexes because male and female rats in the laboratory show similar cooperation levels. Both male and female rats prefer to cooperate, even if they could achieve the same reward individually (Schuster & Perelberg, 2004). Further, if male rats have a choice between obtaining a reward for themselves or for themselves and a partner, they opt for the latter, mutually rewarding option (Hernandez-Lallement, van Wingerden, Marx, Srejc, & Kalenscher, 2015). This suggests that both sexes cooperate, which could be enabled by reciprocity. Indeed, there is evidence that male laboratory rats apply direct reciprocity decision rules (Li & Wood, 2017; Viana, Gordo, Sucena, & Moita, 2010; Wood, Kim, & Li, 2016). However, in these experiments it was not clear whether the focal rats applied generalized instead of direct reciprocity rules.

This is an important difference that may relate to systematic differences in social organization between the sexes. Domestic dogs, *Canis lupus familiaris*, for example, show similar helping levels in a direct and generalized reciprocity task, suggesting that they only use the latter, that is the simpler mechanism for cooperation (Gfrerer & Taborsky, 2017). Moreover, a comparison of the behaviour of wild-type Norway rats with that of laboratory strains of rats

is not straightforward because the latter have been bred for particular purposes since 1906 (Lindsey & Baker, 2006), which has led to behavioural differences between laboratory strains and wild-type rats, for instance in learning ability (Boice, 1972) and aggression (de Boer, van der Vegt, & Koolhaas, 2003). Thus, it is not yet clear whether male wild-type Norway rats apply direct or generalized reciprocal decision rules.

Here we investigated the decision rules applied by male wild-type Norway rats when enabled to reciprocate favours with same-sex partners. In the first experiment, we tested for direct reciprocity. Focal rats first experienced partners either donating food to them altruistically or refusing to help them obtain access to food. Thereafter, the focal rats were enabled to donate food to these partners, which tested for the use of direct reciprocity decision rules. In the second experiment, we investigated whether male rats would donate food according to generalized reciprocity. Focal rats experienced several partners in a row that were either cooperating or defecting; afterwards they could provide food to unknown partners, which they had never met before. In the third experiment, we compared the propensity to use direct or generalized reciprocity rules directly. Now focal rats experiencing cooperating and defecting partners could subsequently donate food to known or unknown partners. Because wild male rats interact prosocially with same-sex partners less often than females do (Calhoun, 1979), we predicted that males would show direct reciprocity if they used any decision rules of reciprocal cooperation at all. In contrast, it is unlikely that males would show generalized responses to help from anonymous partners, because in the natural situation unknown males would pose a severe threat to their monopoly of females and resources.

METHODS

Experimental Subjects and Holding Conditions

We used adult male, outbred, wild-type Norway rats descending from wild-caught individuals (source: Animal Physiology Department, University of Groningen, the Netherlands). The rats were habituated to human handling after weaning and hence did not show any signs of stress when being handled, transported to the experimental cage and exposed to the set-up. They were individually marked with ear punches and housed in groups of four to provide a social environment (Sharp, Zammit, Azar, & Lawson, 2003). The cages (80 × 50 cm and 37.5 cm high) were separated from each other by opaque plastic walls to exclude visual contact between the groups. In accordance with the animal welfare legislation of Switzerland (Tierschutzverordnung Schweiz 04/2008) we enriched the cages with various materials (a wooden house and board, a tunnel, a piece of wood to nibble, a cardboard tube to play with, digging material (wood shavings), nest-building material (hay) and a salt block, as suggested by animal care guidelines (Forbes, Blom, Kostmitsopoulos, Moore, & Perretta, 2007). Food (conventional rat pellets) and water were provided ad libitum. In addition, rats received a grain mix, fresh fruits or vegetables once a day. The ambient temperature was 20 ± 1 °C, with a relative humidity of 50–60%. The light:dark cycle was set to 12:12 h, with lights on at 2000 hours and 30 minutes of dawn and dusk. As rats are primarily nocturnal, all training and experiments were conducted during the dark phase under red light (Norton, Culver, & Mullenix, 1975). The experimental animals had a median weight of 627 g (interquartile range 95 g), and they had no contact with females after weaning, while in laboratory housing and during experimentation.

Pre-experimental Training

The experimental set-up was based on a two-player sequential food exchange task (de Waal & Berger, 2000; Rutte & Taborsky, 2007). Test cages (80 × 50 cm and 37.5 cm high) were divided in half with wire mesh. All focal and partner rats experienced the following training prior to the experiment. First, each rat was placed in one half of the cage and trained to pull a stick that was connected to a movable platform in order to receive a food item (one oat flake). The experimenter moved the platform consistently out of the cage over several training sessions and refilled the platform with a new food reward, teaching the rats to pull the stick in order to reach the reward. In the second part of the training, a training partner was placed in the second cage compartment. From then on, when the rats pulled the platform they did not get a reward but their partner did. Their partner could then return the favour. The roles between donor and recipient were regularly exchanged, and the intervals between these alternations were increased gradually from switching the roles after each pull to switching them after series of pulls lasting up to 7 min, which corresponded to the experimental period (see Dolivo & Taborsky, 2015a for a detailed plan of the training scheme). We determined which individuals pulled most often in the last training session from the groups housed in 10 different holding cages. Afterwards we randomly chose four of these 10 individuals to serve as ‘cooperators’ in the experiment. Four randomly chosen rats were also trained to refrain from pulling by blocking the platform during the 7 min of exposure to the social partner in the training phase. These four rats served as ‘defectors’ in the experiment.

Test Procedure

During the experience phase of the three experiments, focal rats experienced partners that were either providing food to them (cooperators) or not (defectors). This phase was followed by the test phase, where focal rats could donate food to a previously experienced partner in the test for direct reciprocity (experiment 1) or an unknown partner in the test for generalized reciprocity (experiment 2). In the last experiment (experiment 3), rats were tested simultaneously for their propensity to donate food to the same or different partners after having been helped or not.

Experiment 1: Do males cooperate according to direct reciprocity?

During the experience phase of this experiment, focal rats ($N = 23$) experienced either a cooperator or a defector once a day for 7 min (Fig. 1). This experience phase lasted for 10 days, so that each focal rat met its partners five times on consecutive days. The order in which focal rats experienced their two partners was selected randomly, but at the same time we ensured that the last experience was equally often a cooperator and a defector, because the last interaction might have a particularly strong effect on the behaviour of the focal rat in the subsequent test. On the 11th day, we exchanged the roles and focal rats could donate food to the neighbouring compartment for 7 min in three situations: facing either the previous cooperator, the previous defector or an empty compartment. The empty compartment control served to check whether pulling rates most resembled a social food donation or an undirected increase in the propensity to manipulate the apparatus. We randomized the order of focal rats and the order of tests of each focal rat (with cooperator, defector and empty cage). Nevertheless, we ensured that all sequences were tested equally often. All randomizations were done with the Excel command ‘RANDBETWEEN’. The experimenter was blind to the identity of the partner, that is, whether it had cooperated or defected during the experience

phase. Focal and partner rats were unrelated, and they were unfamiliar to each other at the start of this experiment.

Experiment 2: Do males cooperate according to generalized reciprocity?

The second experiment encompassed four treatments, each consisting of 5 experience days followed by 1 test day. The focal rats ($N = 23$) experienced either different cooperating or different defecting partners for 7 min each over 5 consecutive days. For consistency between studies, we used a similar procedure as Rutte and Taborsky (2007) in their test of female rats for generalized reciprocity and presented three different partners on 5 consecutive days, which means that two of these partners were presented to the focal rats twice (Fig. 1). In the cooperator treatment, all partners provided food to the focal rat. In the defector treatment, none of the partners provided any food to the focal rat. On day 6 of each treatment, we allowed focal rats to provide food for 7 min to an unknown partner that they had never met before. Afterwards, both experience phases, that is, with either cooperating or defecting partners, were repeated and in the test phase the focal rats could donate food to an empty neighbour compartment instead of donating food to a conspecific. The empty compartment control again served to check whether pulling rates most resembled a social food donation or an undirected increase in the propensity to manipulate the apparatus. Again, the orders of partners and treatments were chosen randomly using the Excel command ‘RANDBETWEEN’. All treatment combinations were tested equally often during the experiment. In addition, we randomized the test order of focal rats and kept this order stable for the four treatments. The experimenter was blind to the treatment of focal rats during the observations. Focal and partner rats were unrelated and unfamiliar to each other.

Experiment 3: Does partner information increase cooperation?

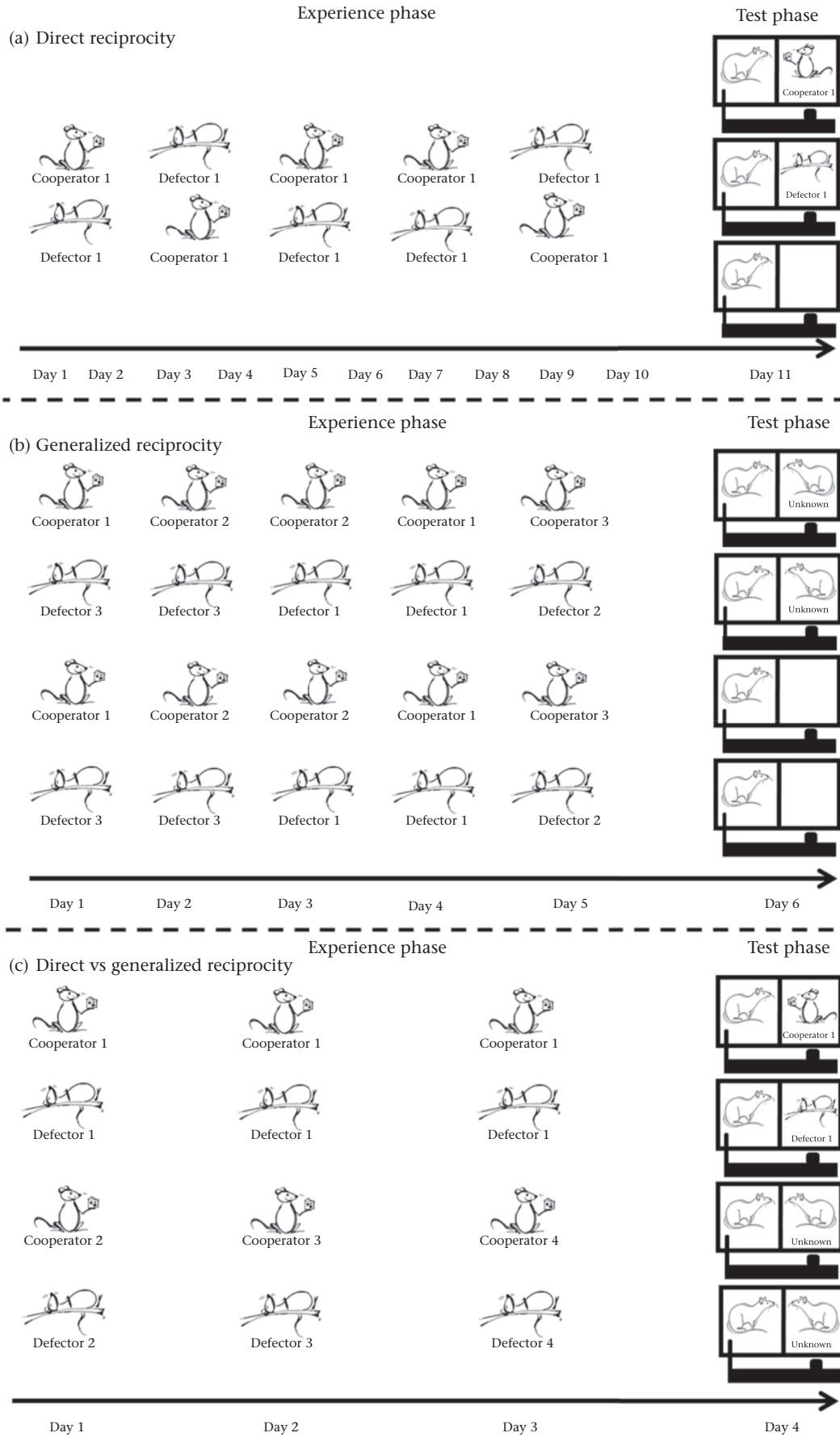
In the third experiment, focal rats ($N = 18$) experienced four treatments in a randomized order (Fig. 1). In all treatments, the focal rat experienced a social partner for 7 min over 3 consecutive days. This partner was either a cooperator or a defector, and it was either always the same partner (direct reciprocity treatment) or always a different one (generalized reciprocity treatment). On the fourth day of each treatment, the focal rat could provide food either to the same partner they were exposed to in the experience phase (direct reciprocity treatment) or to a new, unknown partner (generalized reciprocity treatment). We chose the order of rats, partners and treatments randomly as described above.

Behavioural Data

We counted how often focal rats donated food during the test phase of each experiment by pulling the platform towards the neighbouring compartment. We excluded one focal rat in experiment 1 from the analysis because this rat did not use the apparatus in any of the trials.

Statistical Analyses

All statistical analyses were performed using R (version 2.15.2; R Core Team, 2018; packages ‘lme4’, ‘multcomp’ and ‘stats’; Bates et al., 2015; Hothorn, Bretz, & Westfall, 2008). The focal rat’s identity was included in all generalized linear mixed models (GLMMs) as a random effect because focal rats were tested repeatedly in all three tests as described above. We checked all GLMMs for overdispersion, which never occurred.



Experiment 1: Do males cooperate according to direct reciprocity?

To test whether focal rats reciprocate help according to direct reciprocity, we analysed the total number of donations using a GLMM. We assumed a Poisson distribution as the dependent variable was count data. We included 'partner' (cooperator, defector or absent) as a fixed factor. Because this factor had a significant effect (GLMM: $\chi^2_2 = 10.89$, $N = 22$, $P = 0.004$), we performed a Tukey all-pair comparison, which corrects for multiple testing, to analyse differences between treatments. In addition, we tested whether the amount of help received from cooperators correlated with the amount of help given by focal rats by using a Spearman rank correlation test.

Experiment 2: Do males cooperate according to generalized reciprocity?

To test whether rats cooperate according to generalized reciprocity, we fitted a GLMM, assuming a Poisson distribution. The focal rats' total number of donations was included as a response variable and 'cooperation level' of the partner (cooperating or defecting in experience phase) and 'partner presence' (yes/no) were fixed factors. The interaction between these two factors 'partners being present or absent' and 'partners cooperated or defected' was not significant (GLMM: $\beta = -0.09 \pm 0.18$, $N = 23$, $P = 0.62$). We thus removed the nonsignificant interaction between the two effects (Engqvist, 2005).

Experiment 3: Does partner information increase cooperation?

We used the same analysis to compare the total number of donations to a partner with known cooperation propensity (direct reciprocity treatment) with that to an unknown partner (generalized reciprocity treatment) using a GLMM with an assumed Poisson distribution. The donation rate of focal rats was included as a response variable; the fixed factors were 'partner' (known from the experience phase or unknown) and 'cooperation level' (cooperating or defecting in the experience phase). There was a significant interaction between these factors (GLMM: $\beta = 0.80 \pm 0.34$, $N = 18$, $P = 0.018$). Therefore, we conducted a Tukey all-pair comparison, to test for treatment differences.

Ethical Note

The housing of the animals and the experimental procedure were authorized by the Swiss Federal Veterinary Office under licence BE25/14. There was no possibility of physical contact between the test individuals as wire mesh separated the experimental compartments, and no injuries occurred.

RESULTS

Experiment 1: Do Males Cooperate According to Direct Reciprocity?

Focal rats provided more food to previously experienced cooperators than to defectors (GLMM: $\beta = -0.50 \pm 0.16$, $N = 22$, $P = 0.005$; Fig. 2). There was also a nonsignificant trend for them to provide more food to cooperators than to an empty cage (GLMM: $\beta = -0.32 \pm 0.15$, $N = 22$, $P = 0.074$; Fig. 2), whereas pulling rates

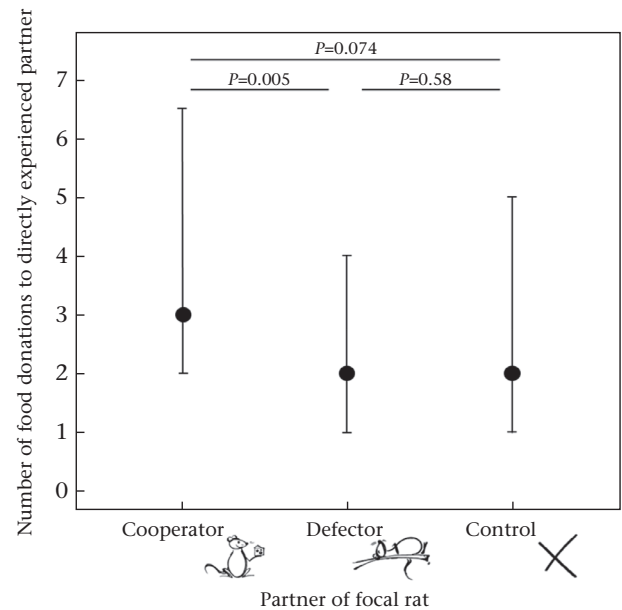


Figure 2. Direct reciprocity: experiment 1. Number of food donations by the focal rat to the current partner in relation to the type of partner previously experienced. The control was an empty neighbouring compartment. Medians are shown with interquartile ranges.

for defectors did not differ from pulling for an empty cage (GLMM: $\beta = -0.17 \pm 0.17$, $N = 22$, $P = 0.58$; Fig. 2). The amount of oat flakes received by focal rats in the experience phase did not correlate with the amount they gave in the test phase of the experiment (Spearman rank correlation: $r_s = -0.05$, $N = 23$, $P = 0.81$).

Experiment 2: Do Males Cooperate According to Generalized Reciprocity?

Experiencing cooperating or defecting partners prior to providing food to an unknown partner did not alter the rats' donation rate (GLMM: $\beta = -0.01 \pm 0.09$, $N = 23$, $P = 0.86$; Fig. 3). Focal rats provided more food to their neighbouring compartment when there was an unknown partner present compared to an empty cage (GLMM: $\beta = 0.35 \pm 0.09$, $N = 23$, $P < 0.0001$; Fig. 3).

Experiment 3: Does Partner Information Increase Cooperation?

Male rats cooperated according to direct reciprocity by providing more food to known cooperating than to defecting partners (GLMM: $\beta = -1.00 \pm 0.26$, $N = 18$, $P < 0.001$; Fig. 4). They did not cooperate according to generalized reciprocity, as experience of cooperation or defection did not influence their decision to donate food to an unknown partner (GLMM: $\beta = -0.20 \pm 0.22$, $N = 18$, $P = 0.82$; Fig. 4). Known defectors received less food than unknown partners after focal rats had experienced cooperating partners (GLMM: $\beta = 0.76 \pm 0.27$, $N = 18$, $P = 0.021$, Fig. 4; see Table 1 for all statistical comparisons).

Figure 1. Experimental set-up of all three tests. (a) In experiment 1, we tested whether rats reciprocate favours according to direct reciprocity. Focal rats experienced two partners in the neighbouring compartment five times each on 10 consecutive days. One partner cooperated by providing food (depicted with a piece of cheese); the other partner provided no food and thus defected (depicted as lying down). On the 11th day, focal rats faced three situations: the previously experienced cooperator, the defector and an empty neighbouring compartment. (b) In experiment 2, we tested whether rats would cooperate according to generalized reciprocity. Here focal rats experienced, over 5 consecutive days, three cooperating partners and could donate food on the next day to an unknown partner. Their donation rate was compared with that toward an unknown partner after experiencing three defecting partners over 5 days. We repeated both treatments with an empty neighbouring compartment as a control. (c) In experiment 3, we directly compared both forms of reciprocity. Focal rats experienced one cooperating partner over 3 days to which they could directly provide food 1 day thereafter (direct reciprocity). The same was done with a defecting partner. They also experienced three different cooperating partners and could provide food to an unknown partner, which resembles a generalized reciprocity set-up. Again, this procedure was repeated with defecting partners. The number of each partner represents an example and the order of the partners was randomized.

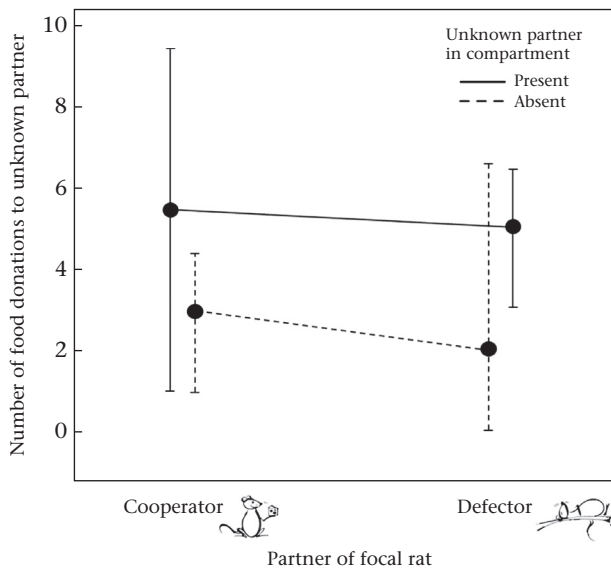


Figure 3. Generalized reciprocity: experiment 2. Number of food donations by the focal rat to unknown partners (solid line) and to empty neighbouring compartments (dashed line) in relation to the type of partner previously experienced. Medians are shown with interquartile ranges.

DISCUSSION

Male wild-type Norway rats cooperated by providing food to each other. They cooperated solely according to direct reciprocity, while decisions to help strangers were not influenced by previous cooperative experiences with anonymous partners, that is, generalized reciprocity was not indicated.

Although male Norway rats have been described as being more aggressive towards each other than females in the wild (Barnett, 1963; Seward, 1944), they can apparently cooperate with one another. In all three experiments, male rats helped other, previously unfamiliar rats by providing food to them. Our findings are in line with research using laboratory strains, where males were found to cooperate peacefully: they provided food to each other in Skinner boxes and other apparatuses (Li & Wood, 2017; Littman, Lanski, & Rhine, 1954; Wood et al., 2016), coordinated movements to gain mutual rewards (Schuster, 2002; Schuster, Berger, & Heidi, 1993) and dived under water to bring food to their cage mates (Colin & Desor, 1986; Grasmuck & Desor, 2002). Together with previous findings (Schweinfurth & Taborsky, 2018a), our study provides evidence that this cooperation among male rats is not an artefact of breeding history, but probably a naturally evolved trait that is also shown in wild-type rats.

Theoretically, male rats might provide help to same-sex partners because they are coerced (Tebbich, Taborsky, & Winkler, 1996) or because they are interdependent (Roberts, 2005; Taborsky et al., 2016). Male rats form a nearly linear hierarchy where dominant individuals might be in the position to coerce subordinates (Adams & Boice, 1983; Blanchard et al., 1988). While female rats have been

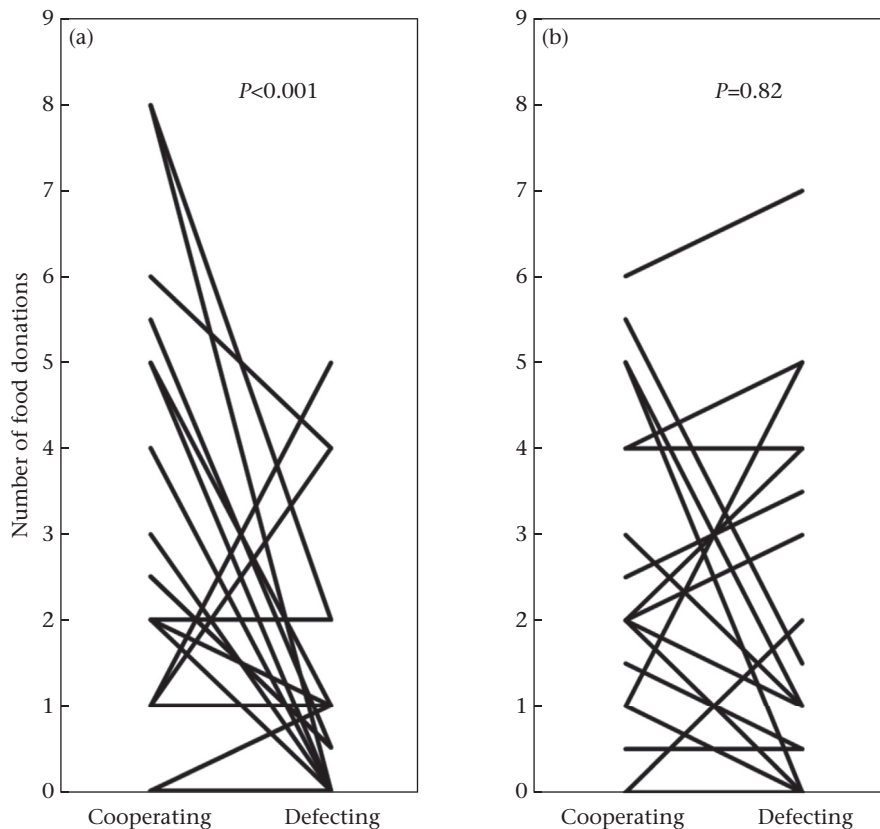


Figure 4. Direct versus generalized reciprocity: experiment 3. Number of food donations by the focal rat to (a) directly experienced cooperators and defectors (direct reciprocity) and (b) unfamiliar partners after experiencing cooperating or defecting partners (generalized reciprocity). Each line represents the behaviour of a focal rat in both conditions. Because some lines overlap, we raised three lines in (a) and four lines in (b) by 0.5; the slopes were unchanged.

Table 1

Comparison of food donations to social partners when information on the previous cooperative behaviour of these individuals was available or not

Comparison	Model estimate [95% confidence interval]	P
Cooperating vs defecting experience (direct reciprocity)	−1.00 [−1.65, −0.35]	<0.001
Cooperating vs defecting experience (generalized reciprocity)	−0.20 [−0.76, 0.37]	0.82
Cooperating experience (direct vs generalized reciprocity)	−0.24 [−0.74, 0.27]	0.64
Defecting experience (direct vs generalized reciprocity)	0.57 [−0.13, 1.26]	0.16
Cooperative experience (generalized reciprocity) vs defecting experience (direct reciprocity)	0.76 [0.09, 1.43]	0.021
Cooperative experience (direct reciprocity) vs defecting experience (generalized reciprocity)	−0.43 [−0.97, 0.10]	0.17

Focal rats experienced cooperating and defecting partners. In the test phase they could either provide food to the same partners they had experienced before, i.e. with known cooperation levels (direct reciprocity), or to unknown new partners (generalized reciprocity). These four treatments were compared with the Tukey all-pair comparison test.

shown to be aggressive towards unresponsive partners in a similar reciprocity experiment (Dolivo & Taborsky, 2015a), this potential explanation for the behaviour of male rats in our experiment is rather unlikely. First, aggressive behaviours such as biting attempts, aggressive body postures or piloerection did not occur during the tests. Second, rats form hierarchies based on direct interactions (e.g. Adams & Boice, 1983). Our rats were unfamiliar to each other, however, so were unlikely to be able to assess the relative rank of their partner. In contrast, male rats might be interdependent like females. For altruistic acts between unrelated individuals to become evolutionarily stable, received and given help may be exchanged reciprocally (Axelrod & Hamilton, 1981; Lehmann & Keller, 2006; Nowak, 2006). Such mutually exchanging partners are somewhat interdependent on each other (Taborsky et al., 2016). Reciprocal cooperation can involve one and the same commodity, as in our study, or several different services (Seyfarth & Cheney, 1984; Taborsky et al., 2016). Female rats have been shown to trade food for allogrooming and vice versa (Schweinfurth & Taborsky, 2018b). Other services that might be traded by male rats for help with obtaining food include support in fighting intruders, shared boundary patrols or allogrooming (cf. Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010; Fruteau, Voelkl, van Damme, & Noë, 2009; Seyfarth & Cheney, 1984).

Male rats cooperate according to direct but not generalized reciprocity, whereas male dogs were found to apply the much simpler generalized reciprocity rules even when tested with previously experienced individual partners (Gfrerer & Taborsky, 2017). Our third experiment showed that rats treated unknown partners better than known defectors, as donation rates for the latter were reduced. This might hint at a strategy where individuals start with a cooperative move when no information about the cooperation propensity of the partner is available, while copying the previously experienced cooperation propensity of the partner once it is known, as for instance in a ‘tit-for-tat’ cooperation exchange (Axelrod & Hamilton, 1981). Importantly, the amount of received and given help was not correlated. This suggests that male rats do not seem to use calculated reciprocity to reward cooperators (Brosnan & de Waal, 2002), which is in line with many other species, including primates (Amici et al., 2014; Pelé, Thierry, Call, & Dufour, 2010) and female rats (Schweinfurth & Taborsky, 2019). Nevertheless, when different qualities of help were provided, female Norway rats were found to reward higher value help with more help (Dolivo & Taborsky, 2015b).

Our results indicate that male rats apply only direct reciprocity rules, whereas female rats apply direct and generalized reciprocity rules under similar training and testing schemes (Rutte & Taborsky, 2007, 2008). This may suggest sex differences in reciprocal cooperation among Norway rats. Further experiments are needed, however, to directly compare animals of both sexes under the same conditions to confirm this hypothesis.

Males may not show generalized reciprocity because they have a different dispersal strategy to females. Although rats typically remain near their birthplace, males disperse more often and further away from their natal territory than females (Gardner-Santana et al., 2009; McGuire, Pizzuto, Bemis, & Getz, 2006). Philopatry is commonly associated with increased cooperation levels, partly due to increased relatedness (Hochberg, Rankin, & Taborsky, 2008; Seyfarth & Cheney, 2012; but see Kümmerli, Gardner, West, & Griffin, 2009 for somewhat divergent observations in *Pseudomonas* bacteria). In most primates, males are the dispersing sex and, in accordance with this, they show little cooperation with same-sex partners (Wrangham, 1979). Nevertheless, there are exceptions where males show higher philopatry and also cooperate at greater levels than females do (e.g. chimpanzees, *Pan troglodytes*: Mitani, 2009; Guinea baboons, *Papio papio*: Patzelt et al., 2014; Barbary macaques, *Macaca sylvanus*: Young, Majolo, Schülke, & Ostner, 2014). Mechanisms associated with the possible connection between philopatry and an increased cooperation propensity include increased relatedness (Hatchwell, 2009) and long-term social relationships (Seyfarth & Cheney, 2012). Increased kinship cannot explain increased cooperation between male rats, however, because kinship reduces rather than increases their helping levels (Schweinfurth & Taborsky, 2018a). Additionally, female rats at least have been shown to lack stable social bonds, despite being the more philopatric sex (Schweinfurth, Neuenschwander, et al., 2017).

In addition, the lack of generalized reciprocity in male rats may be a result of the number of regular interaction partners. Males generally interact with same-sex partners more aggressively than females (Calhoun, 1979), and typically avoid higher ranked individuals (Barnett, 1957). In addition the sex ratios in colonies are female biased (Davis, 1953). This means that males have fewer same-sex interaction partners than females, which may allow them to memorize the partners with whom they had interacted before, enabling to apply direct reciprocity rules.

Female rats may show generalized reciprocity because they have been selected to be more generous in order to increase their reputation. Females show less aggression and more often interact with one another peacefully (Barnett, 1957). Therefore, a reputation for being cooperative might be of higher value to females than to males. Female rats have also been shown to cooperate according to indirect reciprocity (Spahni, 2005), where decisions to help are based on the reputation of interaction partners (Alexander, 1987). Nevertheless, a recent study showed that females do not actively invest in a good reputation by increasing their help levels in the presence of an audience (Schweinfurth & Taborsky, 2016). Thus, processes such as increased image scoring (Nowak & Sigmund, 1998) or a better standing (Sugden, 1986) seem unlikely to explain the greater generosity observed in female than in male rats.

In conclusion, wild-type Norway rat males cooperate by providing food to each other in turn. Thereby, they use direct but

not generalized reciprocity decision rules. A direct comparison showed that they provided more food to unknown partners than to known defectors, which might hint at a strategy by which they start cooperatively and then copy their partner's move. Female rats tested under similar conditions showed both direct and generalized reciprocity. This may imply sex differences in reciprocal cooperation, potentially resulting from different dispersal strategies or different numbers of interaction partners. However, further studies are needed to confirm this hypothesis.

Author Contributions

M.K.S and M.T. conceived the study, designed the experiment and wrote the paper. J.A. and M.K.S. trained the rats. J.A., M.S. and M.K.S. collected the data. M.K.S. carried out the statistical analyses. All authors gave final approval for publication.

Declaration of Interest

The authors declare no competing financial interests.

Acknowledgments

We thank Evi Zwygart for help caring for the animals, Markus Wyman for building the test apparatus, Valentina Balzarini for drawings and Karin Schneeberger and Joachim Frommen for helpful discussions. Further, we thank Amanda Korstjens and two anonymous referees for their insightful and constructive feedback, which has improved the quality of the manuscript. Funding was provided by the Swiss National Science Foundation grants 31003A_156152 and 31003A_176174 to M.T. and P2BEP3_175269 to M.K.S.

References

- Adams, N., & Boice, R. (1983). A longitudinal study of dominance in an outdoor colony of domestic rats. *Journal of Comparative Psychology*, *97*(1), 24–33.
- Alexander, R. D. (1987). *The biology of moral systems*. New York, NY: AldineTransaction.
- Amici, F., Aureli, F., Mundry, R., Amaro, A. S., Barroso, A. M., Ferretti, J., et al. (2014). Calculated reciprocity? A comparative test with six primate species. *Primates*, *55*(3), 447–457.
- Aureli, F., Schaffner, C. M., Verpooten, J., Slater, K., & Ramos-Fernandez, G. (2006). Raiding parties of male spider monkeys: Insights into human warfare? *American Journal of Physical Anthropology*, *131*, 486–497.
- Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*, 1390–1396.
- Backwell, P. R. Y., & Jennions, M. D. (2004). Coalition among male fiddler crabs. *Nature*, *430*(6998), 417.
- Barnett, S. A. (1957). An analysis of social behaviour in wild rats. *Proceedings of the Zoological Society of London*, *130*, 107–152.
- Barnett, S. A. (1963). *The rat—a study in behavior*. Chicago, IL: Aldine.
- Barta, Z., McNamara, J. M., Huszár, D. B., & Taborsky, M. (2011). Cooperation among non-relatives evolves by state-dependent generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1707), 843–848.
- Bates, D. M., Maechler, M., Bolker, B. M., Walker, S. C., Mächler, M., Bolker, B. M., et al. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Blanchard, R. J., Flannely, K. J., & Blanchard, D. C. (1988). Life-span studies of dominance and aggression in established colonies of laboratory rats. *Physiology & Behavior*, *43*, 1–7.
- de Boer, S. F., van der Vegt, B. J., & Koolhaas, J. M. (2003). Individual variation in aggression of feral rodent strains: A standard for the genetics of aggression and violence? *Behavior Genetics*, *33*(5), 485–501.
- Boice, R. (1972). Some behavioral tests of domestication in Norway rats. *Behaviour*, *42*(3/4), 198–231.
- Brosnan, S. F., & de Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature*, *13*(1), 129–152.
- Calhoun, J. B. (1979). *The ecology and sociobiology of the Norway rat*. Bethesda, MD: U.S. Department of Health, Education, and Welfare, Public Health Service.
- Cheney, D. L., Moscovice, L. R., Heesen, M., Mundry, R., & Seyfarth, R. M. (2010). Contingent cooperation between wild female baboons. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(21), 9562–9566.
- Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science*, *296*(5), 69–72.
- Colin, C., & Desor, D. (1986). Différenciations comportementales dans des groupes de rats soumis à une difficulté d'accès de la nourriture. *Behavioral Processes*, *13*, 85–100.
- Darwin, C. (1859). *On the origin of species*. London, U.K.: John Murray.
- Davis, D. E. (1953). The characteristics of rat populations. *Quarterly Review of Biology*, *28*(4), 373–401.
- Díaz-Muñoz, S. L., DuVal, E. H., Krakauer, A. H., & Lacey, E. A. (2014). Cooperating to compete: Altruism, sexual selection and causes of male reproductive cooperation. *Animal Behaviour*, *88*, 67–78.
- Dolivo, V., & Taborsky, M. (2015a). Cooperation among Norway rats: The importance of visual cues for reciprocal cooperation, and the role of coercion. *Ethology*, *121*, 1071–1080.
- Dolivo, V., & Taborsky, M. (2015b). Norway rats reciprocate help according to the quality of help they received. *Biology Letters*, *11*, 20140959.
- Dugatkin, L. A. (2002). Animal cooperation among unrelated individuals. *Naturwissenschaften*, *89*(12), 533–541.
- Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4), 967–971.
- Forbes, D., Blom, H., Kostmitsopoulos, N., Moore, G., & Perretta, G. (2007). *Euroguide on the accommodation and care of animals used for experimental and other scientific purposes*. London, U.K.: Federation of European Laboratory Animal Science Associations.
- Fruteau, C., Voelkl, B., van Damme, E., & Noë, R. (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(29), 12007–12012.
- Gardner-Santana, L. C., Norris, D. E., Fornadel, C. M., Hinson, E. R., Klein, S. L., & Glass, G. E. (2009). Commensal ecology, urban landscapes, and their influence on the genetic characteristics of city-dwelling Norway rats (*Rattus norvegicus*). *Molecular Ecology*, *18*(13), 2766–2778.
- Gfrerer, N., & Taborsky, M. (2017). Working dogs cooperate among one another by generalised reciprocity. *Scientific Reports*, *7*, 43867.
- Grasmuck, V., & Desor, D. (2002). Behavioural differentiation of rats confronted to a complex diving-for-food situation. *Behavioural Processes*, *58*(1/2), 67–77.
- Grinnell, J., Packer, C., & Pusey, A. E. (1995). Cooperation in male lions: Kinship, reciprocity or mutualism? *Animal Behaviour*, *49*, 95–105.
- Hager, R., & Jones, C. B. (2009). *Reproductive skew in vertebrates: Proximate and ultimate causes*. Cambridge, U.K.: Cambridge University Press.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16.
- Hatchwell, B. J. (2009). The evolution of cooperative breeding in birds: Kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 3217–3227.
- Hatchwell, B. J., Gullett, P. R., & Adams, M. J. (2014). Helping in cooperatively breeding long-tailed tits: A test of Hamilton's rule. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*, 20130565.
- Hernandez-Llallemt, J., van Wingerden, M., Marx, C., Srejic, M., & Kalenscher, T. (2015). Rats prefer mutual rewards in a prosocial choice task. *Frontiers in Neuroscience*, *9*, 1–9.
- Hochberg, M. E., Rankin, D. J., & Taborsky, M. (2008). The coevolution of cooperation and dispersal in social groups and its implications for the emergence of multicellularity. *BMC Evolutionary Biology*, *8*(239), 1–14.
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, *23*(4), 707–740.
- Kingma, S. A., Santema, P., Taborsky, M., & Komdeur, J. (2014). Group augmentation and the evolution of cooperation. *Trends in Ecology & Evolution*, *29*, 476–484.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.
- Kümmerli, R., Gardner, A., West, S. A., & Griffin, A. S. (2009). Limited dispersal, budding dispersal, and cooperation: An experimental study. *Evolution*, *63*(4), 939–949.
- Lehmann, L., & Keller, L. (2006). The evolution of cooperation and altruism—a general framework and a classification of models. *Journal of Evolutionary Biology*, *19*(5), 1365–1376.
- Li, G. R., & Wood, R. I. (2017). Male rats play a repeated donation game. *Physiology & Behavior*, *174*, 95–103.
- Lindsey, J. R., & Baker, H. J. (2006). Historical foundations. In C. L. F. M. A. Suckow, & S. H. Weisbroth (Eds.), *The laboratory rat* (2nd ed., pp. 2–52). London, U.K.: Elsevier Academic Press.
- Littman, R. A., Lanski, L. M., & Rhine, R. J. (1954). Studies of individual and paired interactional problem solving behavior of rats (*Mus norvegicus albinus*). *Behaviour*, *7*(2/3), 189–206.
- McDonald, D. B. (1989). Correlates of male mating success in a lekking bird with male–male cooperation. *Animal Behaviour*, *37*, 1007–1022.
- McGuire, B., Pizzuto, T., Bemis, W. E., & Getz, L. L. (2006). General ecology of a rural population of Norway rats (*Rattus norvegicus*) based on intensive live trapping. *American Midland Naturalist*, *155*(1), 221–236.
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640.

- Norton, S., Culver, B., & Mullenix, P. (1975). Development of nocturnal behavior in albino rats. *Behavioral Biology*, 15(3), 317–331.
- Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, 314(5805), 1560–1563.
- Nowak, M. A., & Sigmund, K. (1998). The dynamics of indirect reciprocity. *Journal of Theoretical Biology*, 194(4), 561–574.
- Patzelt, A., Kopp, G. H., Ndao, I., Kalbitzer, U., Zinner, D., & Fischer, J. (2014). Male tolerance and male-male bonds in a multilevel primate society. *Proceedings of the National Academy of Sciences of the United States of America*, 111(41), 14740–14745.
- Pelé, M., Thierry, B., Call, J., & Dufour, V. (2010). Monkeys fail to reciprocate in an exchange task. *Animal Cognition*, 13(5), 745–751.
- Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M., & Bonhoeffer, S. (2005). Evolution of cooperation by generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, 272(1568), 1115–1120.
- Phillips, T. (2017). The concepts of asymmetric and symmetric power can help resolve the puzzle of altruistic and cooperative behaviour. *Biological Reviews*, 93(1), 457–468.
- Quinones, A. E., van Doorn, G. S., Pen, I., Weissing, F. J., & Taborsky, M. (2016). Negotiation and appeasement can be more effective drivers of sociality than kin selection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150089.
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org>.
- Rankin, D. J., & Taborsky, M. (2009). Assortment and the evolution of generalized reciprocity. *Evolution*, 63(7), 1913–1922.
- Ratnieks, F. L. W., & Wenseleers, T. (2008). Altruism in insect societies and beyond: Voluntary or enforced? *Trends in Ecology & Evolution*, 23(1), 45–52.
- Reyer, H.-U. (1984). Investment and relatedness: A cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Animal Behaviour*, 32(4), 1163–1178.
- Roberts, G. (2005). Cooperation through interdependence. *Animal Behaviour*, 70(4), 901–908.
- Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, 5(7), 1421–1425.
- Rutte, C., & Taborsky, M. (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): Direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology*, 62(4), 499–505.
- Schuster, R. H. (2002). Cooperative coordination as a social behaviour: Experiments with an animal model. *Human Nature*, 13(1), 47–83.
- Schuster, R. H., Berger, B. D., & Heidi, H. (1993). Cooperative social coordination and aggression: II. Effects of sex and housing among three strains of intact laboratory rats differing in aggressiveness. *Quarterly Journal of Experimental Psychology*, 46(4), 367–390.
- Schuster, R. H., & Perelberg, A. (2004). Why cooperate? An economic perspective is not enough. *Behavioural Processes*, 66, 261–277.
- Schweinfurth, M. K. (in press). Reciprocity in Norway rats (*Rattus norvegicus*). In A. Kaufman, J. Call, & J. Kaufman (Eds.), *The Cambridge handbook of animal cognition*. Cambridge, U.K.: Cambridge University Press.
- Schweinfurth, M. K., Neuenschwander, J., Engqvist, L., Schneeberger, K., Rentsch, A. K., Gyax, M., et al. (2017). Do female Norway rats form social bonds? *Behavioral Ecology and Sociobiology*, 71(6), 98.
- Schweinfurth, M. K., Stieger, B., & Taborsky, M. (2017). Experimental evidence for reciprocity in allogrooming among wild-type Norway rats. *Scientific Reports*, 7(1), 4010.
- Schweinfurth, M. K., & Taborsky, M. (2016). No evidence for audience effects in reciprocal cooperation of Norway rats. *Ethology*, 122(6), 513–521.
- Schweinfurth, M. K., & Taborsky, M. (2017). The transfer of alternative tasks in reciprocal cooperation. *Animal Behaviour*, 131, 35–41.
- Schweinfurth, M. K., & Taborsky, M. (2018a). Relatedness decreases and reciprocity increases cooperation in Norway rats. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20180035.
- Schweinfurth, M. K., & Taborsky, M. (2018b). Reciprocal trading of different commodities in Norway rats. *Current Biology*, 28(4), 142–143.
- Schweinfurth, M. K., & Taborsky, M. (2019). Rats play tit-for-tat instead of integrating social experience over multiple interactions. Manuscript submitted for publication.
- Seward, J. P. (1944). Aggressive behavior in the rat I—general characteristics, age and sex differences. *Journal of Comparative Psychology*, 38, 175–197.
- Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308, 541–543.
- Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, 63, 153–177.
- Sharp, J., Zammit, T., Azar, T., & Lawson, D. (2003). Stress-like responses to common procedures in individually and group-housed female rats. *Journal of the American Association for Laboratory Animal Science*, 42(1), 9–18.
- Spahni, C. (2005). *Indirect reciprocity in Norway rats (Rattus norvegicus)* (Master thesis). Bern, Switzerland: University of Bern.
- Stieger, B., Schweinfurth, M. K., & Taborsky, M. (2017). Reciprocal allogrooming among unrelated Norway rats (*Rattus norvegicus*) is affected by previously received cooperative, affiliative and aggressive behaviours. *Behavioral Ecology and Sociobiology*, 71, 182.
- Sugden, R. (1986). *The economics of rights, co-operation, and welfare*. Oxford, U.K.: Blackwell.
- Taborsky, M. (1994). Sneakers, satellites, and helpers: Parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, 23, 1–100.
- Taborsky, M. (2016). Cichlid fishes: A model for the integrative study of social behavior. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates studies of ecology, evolution, and behavior* (pp. 272–293). Cambridge: Cambridge University Press.
- Taborsky, M., Frommen, J. G., & Riehl, C. (2016). Correlated pay-offs are key to cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150084.
- Tebich, S., Taborsky, M., & Winkler, H. (1996). Social manipulation causes cooperation in keas. *Animal Behaviour*, 52(1), 1–10.
- Telle, H. (1966). Beitrag zur Erkenntnis der Verhaltensweise von Ratten, vergleichend dargestellt bei *Rattus norvegicus* und *Rattus rattus*. *Zeitschrift für Angewandte Zoologie*, 53, 129–196.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46(1), 35–57.
- Viana, D. S., Gordo, I., Sucena, E., & Moita, M. M. (2010). Cognitive and motivational requirements for the emergence of cooperation in a rat social game. *PLoS One*, 5(1), e8483.
- de Waal, F. B. M., & Berger, M. L. (2000). Payment for labour in monkeys. *Nature*, 404, 563.
- Weidt, A., Lindholm, A. K., & König, B. (2014). Communal nursing in wild house mice is not a by-product of group living: Females choose. *Naturwissenschaften*, 101, 73–76.
- Weitekamp, C. A., & Hofmann, H. A. (2017). Neuromolecular correlates of cooperation and conflict during territory defense in a cichlid fish. *Hormones and Behavior*, 89, 145–156.
- Wood, R. I., Kim, J. Y., & Li, G. R. (2016). Cooperation in rats playing the iterated Prisoner's dilemma game. *Animal Behaviour*, 114, 27–35.
- Wrangham, R. W. (1979). On the evolution of ape social systems. *International Social Science Council*, 18(3), 336–368.
- Yee, J. R., Cavigelli, S. A., Delgado, B., & McClintock, M. K. (2008). Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosomatic Medicine*, 70(9), 1050–1059.
- Young, C., Majolo, B., Schülke, O., & Ostner, J. (2014). Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques. *Animal Behaviour*, 95, 23–32.