

# A positive feedback loop between sociality and social competence

Barbara Taborsky 

Behavioural Ecology Division, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

## Correspondence

Barbara Taborsky, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland.

Email: barbara.taborsky@iee.unibe.ch

## Funding information

Swiss National Science Foundation

Editor: Redouan Bshary

## Abstract

The social environment of animals influences individual social decisions, which in turn feeds back on the social environment. The two halves of this feedback loop are rarely studied in conjunction. Here, I propose and review evidence for a positive feedback loop between sociality and social competence. Because social competence increases the performance during social encounters of all kinds, positive feedback between selection on social competence and sociality seems plausible. In the first part, I present evidence that social competence is an evolving trait: it exhibits consistent variation between individuals, has fitness consequences and is genetically or non-genetically transmitted across generations. In the second part, I propose that the feedback loop between sociality and social competence may be mediated by a link to dispersal propensity. I review the available evidence for this possible mechanism: higher social competence and philopatry may be part of the same social phenotype, and in some social species dispersal propensity is heritable. Finally, I discuss the evolutionary consequences of the proposed mechanism for the scenarios that social phenotype is transmitted genetically or plastically across generations.

## KEYWORDS

cooperative breeding, dispersal, heritability, non-genetic inheritance, philopatry, social behaviour

## 1 | INTRODUCTION

Socially living animals may have hundreds of social encounters a day with conspecifics. Individuals that are able to integrate social information about the context of an encounter, the social position, state and motivation of a social partner relative to one's own, and consequently, to express appropriate social behaviours should accrue fitness benefits compared to individuals not using social information. The ability of an individual to optimize its social behaviour depending on the available social information is referred to as social

competence (Oliveira, 2009; Taborsky & Oliveira, 2012). Benefits from a higher social competence can include, for instance, more efficient or faster solutions of conflicts over resources, thereby saving energy and time (Lehner et al., 2011) or reducing the risk of injuries (Camerlink et al., 2019). Social competence may help, for instance, to attract group mates to a cooperative task in order to gain a resource (Dolivo & Taborsky, 2015; Schweinfurth & Taborsky, 2018), or it may promote social tolerance by conspecifics (Fischer et al., 2017; Taborsky et al., 2012). The benefits of a higher social competence should increase with the number of social encounters an individual

[The copyright line for this article was changed on 15 September 2021, after original online publication.]

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2021 The Authors. *Ethology* published by Wiley-VCH GmbH.

has each day. Social competence also comes with costs, which may outweigh the potential benefits, in particular, when animals pursue a predominantly solitary lifestyle.

Because social competence pertains to behaviours in the entire social domain, it is an important determinant of social decisions made by individuals. Social decisions can affect emergent properties at the population level like the structure of societies. Social structure, in turn, can feedback on individual behaviour and social decisions (Cantor et al., 2020). Feedback loops (i) from individual behaviour to the structure of societies and (ii) from society back to behaviour have rarely been considered in conjunction (Cantor et al., 2020). Here, I develop the hypothesis that, through a positive feedback loop, selection for sociality can promote social competence and vice versa. This hypothesis was first put forward by Taborsky and Oliveira (2012). If the environment favours sociality this selects for individuals with higher social competence; and because a higher social competence allows for better outcomes (more benefits, lower costs) of social encounters, individuals will tend to be more social (e.g. engage in more encounters, join larger groups). This will increase selection pressure for evolving even higher social competence, resulting in a positive feedback loop (Figure 1a).

Here, I will (1) investigate the evolutionary foundations of this positive feedback, and (2) propose a potential evolutionary mechanism underlying this feedback loop, which assumes that philopatric tendencies and social competence are linked. In part 1, I review evidence that social competence is an evolving trait, that is, there is variation in social competence selection can act on, social competence has fitness consequences and social competence is transmitted across generations, either genetically or non-genetically. The variation and the costs and benefits of sociality have been extensively reviewed elsewhere (e.g. Bourke, 2011; Koenig & Dickinson, 2016; Schradin, 2013).

In part 2, I propose that a positive feedback between social competence and social evolution may arise if socially competence is linked to philopatry. For instance, if in cooperatively breeding societies environmental conditions, such as limited space for breeding territories or high predation, favour philopatry, and if these tendencies are genetically or non-genetically transmitted to the next generation (cf. Kasper et al., 2017a), group size will increase over time. In

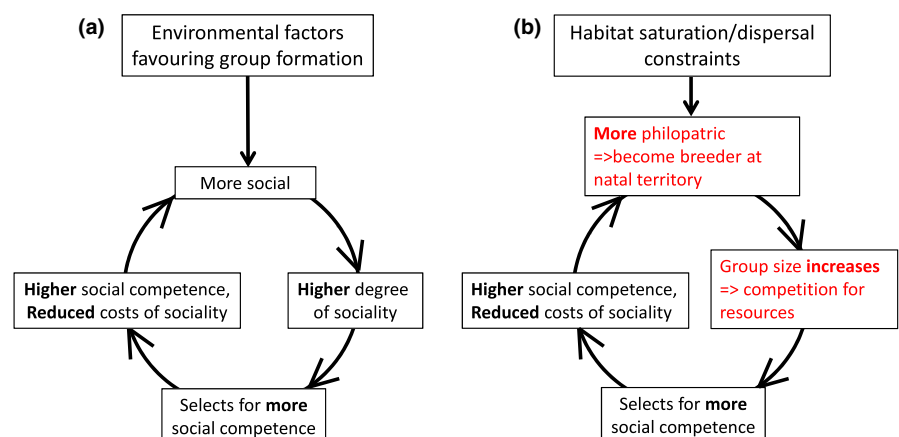
societies, in which members have individualized relationships, group size is a good proxy of the number and diversity of social interactions (i.e. social complexity, Morrison et al., 2020; Taborsky, 2016). With larger group sizes, within-group conflicts and competition will increase, which will select for higher social competence as it allows solving conflicts more efficiently. More socially competent individuals thus incur reduced costs of sociality and may tend to stay as subordinates in their natal territory and queue for the breeder position (Fischer et al., 2017), resulting in even further group size increases (Figure 1b). Conversely, if the environment favours dispersal and dispersive tendencies are transmitted to offspring, group sizes will remain small, which results in weakened selection for social competence.

## 2 | PART I: SOCIAL COMPETENCE AS EVOLVING TRAIT

### 2.1 | Variation

Social competent behaviour is widespread in animals. For instance, information about own fighting performance in previous fights is frequently used during subsequent contests; winner-loser effects are ubiquitous across a wide range of taxa (Rutte et al., 2006). Results from a recent evolutionary model suggest that they result from generalization learning during hierarchy formation (Leimar, 2021). Another example is social eavesdropping, which occurs when individuals observe contests between two conspecifics, and later adjust their own behaviour when interacting with one of the observed individuals (Oliveira et al., 1998; Tibbetts et al., 2020). Likewise, interacting animals may respond to the presence of observing bystanders ("audience effect") by changing their social behaviour according to audience type and social context (e.g. Doutrelant et al., 2001; Pinto et al., 2011). Finally, also cooperation conditional on previously received help by other individuals (e.g. by direct or indirect reciprocity) requires social competence (Taborsky et al., 2016).

To be an evolving trait, social competence needs to express some persistent individual variation selection can act on, and which may depend on the frequency of other behavioural strategies



**FIGURE 1** (a) Proposed positive feedback between evolution of social competence and sociality. (b) Hypothesis proposing that the positive feedback in panel (a) is driven by a link between philopatry and social competence (text in red highlights the differences from panel (a))

present in a population (frequency-dependent selection). This is suggested by the results of an extended hawk-dove game (see Maynard Smith 1982) investigating the benefits from using social information gained from dyadic contests of two individuals. The results of the extended model suggest that information use is most beneficial if the frequencies of hawks and doves, two strategies that do not use social information, occur at equilibrium frequencies (Johnstone 2001).

Persistent variation in social competence can have a genetic basis or can arise during ontogeny. Genetic variation appears to exist in humans as suggested by twin studies (Kuo et al., 2004; McGuire et al., 1999; see also section "inheritance"). In contrast to the sparse evidence for genetic variation in social competence, there is robust support of the ontogenetic origin of variation in social competence in several vertebrates (reviewed in Taborsky & Oliveira, 2012 and Taborsky, 2016a). Variation in social competence has been induced by environmental parental effects (Arnold & Taborsky, 2010; Bastian et al., 2003; Curley et al., 2009; Fischer et al., 2015; Levy et al., 2003; Nyman et al., 2017; Taborsky et al., 2012), or by varying the social rearing conditions animals incur during early life (Adkins-Regan & Krakauer, 2000; Branchi et al., 2006; Camerlink et al., 2019; Fischer et al., 2015) or adulthood (White et al., 2010). Ontogenetically induced variation of social competence can affect, among others, the quality of maternal behaviour towards pups in the nests (Curley et al., 2009), how fast or efficient an individual finds its position in a social hierarchy (Branchi et al., 2006; 2009; Fischer et al., 2015; Taborsky et al., 2012), which rank is achieved (Bastian et al., 2003), and appropriate courtship behaviour (Adkins-Regan & Krakauer, 2000; White et al., 2010).

Social competence does not represent a specialization to perform well in a particular social task, but it pertains to the entire social domain (Taborsky & Oliveira, 2012). Thus, it leads to better social performance across social contexts. Variation in social competence across different social contexts has been demonstrated in communally breeding laboratory mice and cichlid fish. Mice reared in communal nests, where they were exposed to more social contacts, showed more appropriate social behaviours as adults in the contexts of dominance interactions and brood care, compared to single-mother reared mice (Curley et al., 2009). After being reared with parents and helpers, young of the cooperatively breeding cichlid *Neolamprologus pulcher* behaved more appropriately in two different competitive contexts (Arnold & Taborsky, 2010; Nyman et al., 2017; Taborsky et al., 2012; Box 1) and when striving for acceptance as helper by an unfamiliar breeder pair (Fischer et al., 2017; Taborsky et al., 2012), compared to individuals reared among siblings only. Furthermore, *N. pulcher* reared in large social groups with parents and many helpers adopted a subordinate role in a hierarchy more readily later in life than fish reared in small groups (Fischer et al., 2015). Unexpectedly, the early social environment of *N. pulcher* influenced variation in the expression of appropriate social behaviours, but the expression of non-appropriate behaviours such as fleeing from aggression, which elicits chasing by the opponents and can result in complete eviction from a territory, did not differ between fish with different early social experiences (Arnold & Taborsky, 2010).

Of course, not every variation of early social experience results in an ability to show more appropriate behaviours across social contexts (i.e. higher social competence). Early life conditions may also induce quite specific, potentially adaptive effects. For instance, laboratory rats that received high-quality maternal care in the pup stage directed more high-quality care also to their own offspring (Francis et al., 1999; Liu et al., 1997), which can be considered appropriate social behaviour. However, they were less competitive during social play and were less able to compete aggressively over a scarce resource (Parent et al., 2013), suggesting they used social behaviour inappropriately in competitive contexts.

## 2.2 | Fitness consequences

### 2.2.1 | Benefits

Having higher social competence should be beneficial during any social encounter. As it improves social performance, higher social competence should yield incremental benefits, however, small, from each social encounter (relative to individuals with lower social competence). Most animals are involved in some social encounters during their lives, at least during mating, during which they could benefit from this ability. Still, as social competence also bears costs to develop and maintain the machinery for social information processing (see "Costs" below), the more social encounters an individual has, the more it can benefit from higher social competence. Therefore, the benefits of social competence are expected to be most pronounced in socially living species, where almost all behaviours during daily life, including acquiring and defending resources, predator evasion, and rearing offspring, involves social interactions.

Benefits of social competence arise if using social information aids to solve conflicts with conspecifics more efficiently. For instance, Norway rats (*Rattus norvegicus*) which previously had won a contest, attacked other rats in future contests more readily, and won more likely after a shorter time despite reducing their aggression sooner; accordingly, previous losers received less aggression despite showing less submissive behaviour (Lehner et al., 2011). Also, winner effects in mice of the genus *Peromyscus* reduced "losing behaviour" (defined by the authors as retreats, jumps away and freezes) in winners, but induced more losing behaviour in their opponents, thereby increasing the efficiency of winners to solve contests (Fuxjager et al., 2011). Finally, benefits may arise from "dear-enemy effects," when individuals reduce territorial defence towards familiar neighbours met in a familiar place, thereby saving time or energy. American red squirrels (*Tamiasciurus hudsonicus*) reduced their territorial behaviour and instead spent more time at their nest when being surrounded by familiar neighbours (Siracusa et al., 2019). Benefits may also be achieved by accounting for social information obtained by observing conspecifics (eavesdropping, Oliveira et al., 1998), or by being responsive to being observed: When courting females at a lek, male sage grouse (*Centrocercus urophasianus*) enhance copulation success when adjusting their

**BOX 1 Case study: Social phenotypes in the cooperatively breeding cichlid *Neolamprologus pulcher***

*N. pulcher* live in social groups of 3 to  $\geq 20$  group members. A large, dominant breeder pair is assisted in raising its offspring by related and unrelated subordinate helpers, which engage in direct brood care (egg cleaning and fanning), territory maintenance and defending the territory against predators and space competitors (Taborsky, 2016b). Groups are structured by a size-dependent, linear hierarchy. Until sexual maturity around an age of 1 year, all subordinate group members delay dispersal from their natal groups. In the wild, *N. pulcher* can reach adult ages of up to 6–8 years (Jungwirth et al., *subm*). Many subordinates stay as helpers at the natal territory long after sexual maturity, whereas others disperse rather soon afterwards. Subordinates appease dominant group members, which direct aggressive behaviour towards them, either by showing submissive behaviour more readily or by engaging more in helping behaviour (e.g. Bergmüller & Taborsky, 2005). The propensities to show the submissive or helping social phenotype are consistent within individuals over time (i.e. repeatable) and negatively correlated (Kasper et al., 2017b).

During three long-term rearing experiments (Table A), *N. pulcher* were reared either with parents, unrelated helpers and same-aged siblings, which reflects a natural group composition ("with older fish" or "+F" treatment) or only with same-aged siblings, which represents a socially deprived rearing environment ("without older fish" or "-F" treatment). Individuals from the +F treatment had a higher social competence, pursued more often a philopatric life history and eventually had a higher reproductive output (Table A). Fish from the -F treatment showed the opposite traits. A long-term field study with marked individuals revealed that also in the wild, philopatric fish, which inherit a breeder position later on, have higher lifetime fitness than dispersers do (Jungwirth et al., *subm*). While the mechanistic underpinnings of animal social competence are still poorly understood, there is experimental evidence that in *N. pulcher* social competence is related to the physiological stress axis. Pharmacological manipulation of the stress axis by applying a blocker of the most important receptor of the glucocorticoid hormone "cortisol" modulated socially competent behaviour in a competitive social challenge (Nyman et al., 2018). In line with this, -F and +F fish differed in various parameters related to stress axis regulation (Antunes, Reyes-Contreras et al., 2021; Nyman et al., 2017).

**TABLE A** Summary of three rearing experiments manipulating the early social environment of *N. pulcher* during their first two months of life. \*Only results of +F and -F treatments in the absence predator cues are listed

Age	Status of focal fish	Encounter with	+F treatment (rel. to -F)	Reference
1–2 month	unknown	same aged siblings	more submission	Arnold & Taborsky, 2010*
1–2 month	unknown	same aged siblings	more aggression	Arnold & Taborsky, 2010, Fischer et al., 2017*
3 month, 4.5	subordinate	same sized peer	more submission per received aggression	Arnold & Taborsky, 2010
3 month	dominant	same sized peer	more threat behaviour	Arnold & Taborsky, 2010
4.5 month	alone		higher brain gene expression of GR, egr1, and BDNF	Nyman et al., 2017
4.5–11 month	winner	same sized peer	more overt aggression	Taborsky et al., 2012
4.5–11 month	loser	same sized peer	more submission	Taborsky et al., 2012
5 month, 7.5–13 month	subordinate	unfamiliar breeder pair	more submission, higher tolerance in a group	Fischer et al., 2017*, Taborsky et al., 2012
10 month	subordinate	unfamiliar breeder pair	less egg care	Fischer et al., 2017*
3 years	subordinate	choice between breeder pair (philopatry) vs. mating partner (dispersal)	more philopatric	Fischer et al., 2017*
4 years	breeder	mating partner of same early experience	more and larger eggs	Antunes et al., 2020*
8 years	alone		higher baseline cortisol, (but no difference in stress response)	Antunes, Reyes-Contreras et al., 2021

courtship effort to the presence (but not to the attention) of females (Perry et al., 2019).

Consistent differences in social competence acquired by learning during social encounters either during development or as adults can result in fitness benefits. When keeping adult brown headed cowbirds in groups of a dynamic composition, where members of the group were exchanged regularly (White et al., 2010), or adults were kept mixed with juveniles (White et al., 2002), adult males had a higher courtship success, singing competence and copulation success later on compared to adult males kept in socially less diverse groups. Being reared in a more complex or diverse social environment also aided to establish social hierarchies faster (*Mus domesticus*, Branchi et al., 2006, Camerlink et al., 2019), achieve higher tolerance as subordinates by dominants in social groups (*N. pulcher*, Taborsky et al., 2012, Fischer et al., 2015, 2017) or even to obtain a higher rank (*Macaca mulatta*, Bastian et al., 2003). Moreover, *N. pulcher* cichlids reared in small, semi-natural social groups solved contests in a shorter time (Arnold & Taborsky, 2010) than fish reared only with siblings but without parents and helpers. This should translate into a fitness benefit for group-reared fish of reduced energy expenditure, as aggression against conspecifics increases metabolic rate by almost the fivefold of the standard metabolic rate in *N. pulcher* (Grantner & Taborsky, 1998). When competing with a same-sized conspecific over a shelter, group-reared *N. pulcher* did not win more often, but group-reared losers were tolerated closer to the shelter and were less often evicted from a winner's territory. These fitness gains of competing *N. pulcher* were owing to the ability of group-reared losers to show more submission towards winners (Taborsky et al., 2012; Table A).

The fitness benefits reviewed in the previous paragraph have one feature in common: The benefit an individual can accrue during a single social interaction is comparatively small. Showing more appropriate social behaviour does not enable an individual a "winner-takes-it-all" type of benefit. It does not help to obtain a mate, as opposed to having no mate at all. It does not decide over winning or losing a fight. However, it results in small, incremental benefits which, when accumulating over hundreds of social encounters over the life time, will add up to a substantial fitness increase. I argue that incremental rather than large benefits per social encounter are expected. If social competence were leading to very large benefits per encounter, selection on social competence would be extremely strong and variation in this trait would erode quickly. Directional selection towards more social competence would also be attenuated, if this ability has costs, which are addressed in the next section.

## 2.2.2 | Costs

By definition, social competence involves the processing of social information (Oliveira, 2009; Taborsky & Oliveira, 2012). This means social competence is based on a number of lower-level cognitive traits, including the perception, encoding, storage and retrieval of information in the brain (Varela et al., 2020). Besides the digestive tract, the

brain is most energy-demanding organ in the body (Laughlin et al., 1998). Consequently, if social competence requires a higher computing power of the brain and thus more expensive neural tissue, this gives rise to energetic developmental and maintenance costs. For instance, in cleaner wrasses *Labroides dimidiatus*, which adjust their social information use to the presence of conspecific and clients in dependence of local abundance (Triki et al., 2019), forebrain size increased with population densities are high (Triki et al., 2020). Interestingly, however, potential cost of an increase in neural tissue in certain brain parts in response to social cues may be partly or fully compensated by a parallel reduction of the size of other brain regions (Fischer et al., 2015; Triki et al., 2020).

Also, the time to acquire social competence is supposedly an important cost factor during development. Juvenile *N. pulcher* appear to learn how to behave appropriately by interacting with their same-aged peers. Group-reared fish, which become more socially competent, engage in significantly more agonistic and submissive interactions with their siblings at very young age than do young raised without older group members. It is possible that young growing up in the presence of guarding adult fish can afford to invest more time in learning the adequate social responses towards conspecific encounters, a time costs young growing up without guards might not be able to pay as they have to be more vigilant (Arnold & Taborsky, 2010). Also cowbirds, which displayed a more attractive courtship display after being kept in more diverse social groups (White et al., 2002, 2010) may have incurred time costs while learning to produce higher quality courtship displays.

Besides costs caused by developing and maintaining social competence, the flexible adjustment of social behaviour to context itself can be costly, both in terms of energy and/or time ("production costs"; De Witt et al., 1998). In *N. pulcher*, socially competent individuals express a higher rate of submissive displays per received aggression by a dominant peer or a breeder (Arnold & Taborsky, 2010, Nyman et al., 2017, Table A), which effectively reduces conspecific aggression. However, submissive displays are energetically costly: these displays raise the energy expenditure by roughly six times the standard metabolic rate (Grantner & Taborsky, 1998), an increase of energy expenditure equivalent to the maximum metabolic rate (MMR) achieved after the most intensive work possible as measured in other fish (Rosewarne et al., 2016).

Because of energetic and temporal maintenance and production costs of social competence, higher social competence may have to be traded off against other, non-social competences, although it is as yet unclear how these trade-offs may look like. As some costs (time costs during acquisition, energetic costs to develop an information processing machinery) have to be paid only once, typically at the beginning of life, we should predict to find higher social competence and more variation in social competence in animals with a social lifestyle. Once they have paid the initial costs, they can reap the incremental benefits per social encounter more often than animals with predominantly solitary lifestyle. Ideally, this prediction would be tested within a species, where populations live in environments with either more or less social interactions. Such comparison has



been done in the cleaner wrasse: living on intact, continuous reefs these fish have more than twice as many interactions with clients a day compared to cleaners living on isolated reef patches. Audience effects, which modulate the willingness of these fish to feed against a food preference, were significantly stronger and more variable in individuals inhabiting the continuous reefs compared to individuals from patch reefs (Wismer et al., 2014), suggesting that in the population with a higher social encounter rate flexible adjustment to social information plays a greater role.

## 2.3 | Inheritance

### 2.3.1 | Quantitative genetic studies

Evidence of a heritable, genetic basis of social competence in humans, investigated by questionnaire studies of twins, produced partly contradictory results. A study of same-sex monozygotic and dizygotic twins, full-siblings, half-siblings and stepsiblings detected significant heritable genetic variance ( $h^2$ ) of about 0.5 during adolescence. Interestingly, the non-shared experiences of siblings explained an almost equal magnitude of variance, whereas there were almost zero effects of the environment shared by twins or siblings (McGuire et al., 1999). A similar study with adolescent twins and siblings pairs found sex differences in the heritability of social competence: while in boy pairs heritability was again around 0.5, in girls it was on average only 0.24; these differences were not statistically significant, however. The shared environment explained about 50% of the variance in girls but only 20% in boys, whereas the non-shared environment explained a bit less than 30% of the variance in both sexes (Kuo et al., 2004). Finally, in a twin study targeting a much earlier age of kindergarten children reported an overwhelmingly strong effect of the shared environment (70%), which was attributed to early parental support, whereas there was no evidence for genetic heritability (Roisman & Fraley, 2012). The results for high vs absent additive genetic variance are difficult to reconcile, whereas the relative higher impact of the non-shared environment on social competence in higher-aged children (Kuo et al., 2004; McGuire et al., 1999), as compared to the shared environment, might possibly be explained by increasing extra-family experiences of growing-up adolescents.

In non-human animals, the variance components explaining social competence have not yet been studied. However, several quantitative genetic studies have partitioned variance components (see Kruuk & Hadfield, 2007 for methods) aiming at explaining the expression of *particular* social behaviours. These studies identified typically no, weak or moderate heritable genetic variation ( $h^2$ ) for specific social behaviours. For instance, there was moderate to low heritability for aggression in western bluebirds (*Sialia mexicana*, Duckworth & Kruuk, 2009), greylag geese (*Anser anser*, Weiss & Foerster, 2013) and spiders (*Nuctenea umbratica*, Kralj-Fiser et al., 2019), and very weak, but significant, heritability for aggression in crickets (Santostefano et al., 2017). In contrast, there was no evidence for any genetic heritability in four aggressive behaviours and

in submissive behaviour in *N. pulcher* (Kasper et al., 2017b, 2019). Among the tested social behaviours, only one affiliative behaviour of subordinates towards dominant was moderately heritable in these cichlids (Kasper et al., 2019). This finding is interesting in connection with social competence, as affiliative behaviour can be considered as appropriate in the context it is expressed: it aids to improve the conflict-laden relationship between subordinates and the dominants.

### 2.3.2 | Inheritance through non-genetic parental effects

Quantitative genetics studies did not only show that behaviours are genetically heritable to a quite varying degree, but they also identified non-genetic variance components explaining social behaviour, including non-genetic parental effects. For instance, a weak but significant effect of maternal identity on affiliative behaviour was shown in *N. pulcher* (Kasper et al., 2019). Through parental effects, social behaviour tendencies in parents, such as the quality of parental care behaviour, may be transmitted to offspring (e.g. Meaney & Szyf, 2005). Opposite to genetically heritable effects, non-genetic parental effects on social behaviour can be temporary and stage-specific: parental effects on aggression and dominance rank were particularly pronounced in juvenile grey lag geese, but almost absent in adults where the effects of the permanent environment were more prominent (Weiss & Foerster, 2013). This is in line with the observation that parental affects may fade away with age (Lindholm et al., 2006).

Non-genetic inheritance of social competence can occur prenatally, by parental effects on ova, zygotes and developing embryos, or postnatally by parental behaviour on offspring, or both (e.g. Groothuis & Taborsky, 2015 and Taborsky, 2017 for review). For instance, cooperatively breeding cichlids laying eggs in large groups with many helpers reduce their egg size (Taborsky et al., 2007) and egg-mediated parental effects in dependence of helper number also modulated offspring social competence in *N. pulcher* (Fischer et al., 2015).

Summarizing Part 1, evidence suggests that social competence is an evolving trait: it exhibits consistent variation, it affects fitness, and it has high potential to be heritable from one generation to the next. Although the inheritance of social competence is still greatly understudied, the existing evidence suggests there may be at least weak to moderate genetic heritability of social competence and a strong potential for non-genetic inheritance through parental effects.

## 3 | PART 2: POSITIVE FEEDBACK BETWEEN SOCIAL COMPETENCE AND SOCIALITY

This part discusses the possible mutual evolutionary relationship between social competence and sociality, and reviews the available evidence. I will focus here on species that live in societies, defined

as animals living in permanent groups, having individualized relationships between group members depending on their status, state and/or relatedness (see also Glossary in Taborsky et al., 2021). The core of the argument about the mutual relationship between social competence and sociality considers the following: (1) When environmental conditions are in place that favour sociality, being more social, results in positive selection for higher social competence. This is because with increasing sociality individuals face more and/or more diverse social interactions (i.e. social complexity, Taborsky, 2016); in particular, social competition and conflicts increase. (2) Social competence improves the performance in social encounters and reduces the costs of sociality. (3) Therefore, social competence facilitates the evolution of even higher levels of sociality (Figure 1a). Thus under environmental conditions favouring sociality in the first place, there will be concurrent positive selection on social competence and on sociality that reinforce each other. As a consequence, group sizes will increase until reaching values near (even beyond, Lerch & Abbot, 2020) the optimal group sizes in a given species and environment. Focusing on group size as measure of sociality is of course a gross oversimplification of the existing diversity of animal social organizations (Schradin, 2013), but is used here for illustrative purposes. Group size can be considered as suitable proxy for social complexity in societies organized in permanent groups with individualized relationships, which are the focus in this paper (see above). Group size may be unrelated to social complexity, however, when individualized relationships are absent, such as in fish schools or some ungulate herds.

The feedback outlined in Figure 1a does not explain, however, *how* groups increase in size. Here, I propose that this can happen when social competence and philopatry are linked (Figure 1b), that is being part of the same individual social phenotype. Several environmental factors are known to influence the reproductive and survival prospects inside or outside the natal territory, and thereby the decisions of animals whether to remain philopatric or whether to disperse. Philopatry is favoured when possible breeding habitats are saturated (Emlen, 1982; Komdeur, 1992) or when the risk of dispersal, for instance, due to predation (Groenewoud et al., 2016; Heg et al., 2004), is high. Philopatry is also favoured as result of local adaptation (e.g. Starrfelt & Kokko, 2012). If the propensity to be philopatric is transmitted to the offspring, over time groups will increase in size. At the same time, within-group competition will increase. This again will lead to positive selection on social competence, facilitating social interactions and reducing costs of competition (Figure 1b).

Here, I review the evidence for this hypothesis. There are two questions to be investigated. (i) Are social competence and philopatry, and conversely, low competence and dispersal part of the same social phenotype? Animal social competence has still been studied rather rarely, and almost never in conjunction to dispersal (but see Fischer et al., 2017). Because of this unfortunate lack of comparative evidence, I will review the links between social behaviour tendencies of individuals (aggressive, submissive, affiliative and cooperative) and their dispersal propensity across animal societies and I will discuss how these social phenotypes may reflect

social competence. (ii) What is known about heritability of dispersal propensity, either genetically or non-genetically. After reviewing evidence for these two questions, I will discuss their evolutionary consequences.

### 3.1 | Is there a link between social competence and dispersal?

A literature search revealed that social competence or single social skills thought to contribute to social competence have been related most often to sociopositive and cooperative behaviours, but occasionally also to higher aggression and dominance (Higley et al., 1996). In over 30 primate species, several other mammals and one bird, the existence of reconciliation, third party post-conflict affiliation and/or consolation behaviour were reported as indicators of high social competence (reviewed in Farooqi & Koyama, 2016). Furthermore, a higher tolerance towards unfamiliar conspecifics (Gennuso et al., 2018), fairness when sharing a resource (Schank et al., 2018), response to other's needs (Dreiss et al., 2017) and cooperation during predator inspection (Hesse et al., 2015), or simply aggregation and sociability (Schausberger et al., 2017) have been associated with social competence in species ranging from invertebrates to mammals. Finally, a lack of social competence has been diagnosed in individuals showing inappropriate aggression, for example after affiliative approach (Kempes et al., 2008) or overly expressed aggression (Toth et al., 2008).

From summarizing this literature, one might conclude that social competence always entails amicability and/or cooperation and low aggression. Yet, social competence is a holistic concept of social behaviour, which integrates the performance across functional contexts. It includes amicability and cooperation as well as competing aggressively for resources (Bshary & Oliveira, 2015; Taborsky & Oliveira, 2012) as long as the respective social behaviour expressed during an encounter is appropriate given available social information. Thus, the flexible adjustment of behaviour is important, not the propensity to show a particular behaviour more often than another. One may still argue though that in general, social competence may play a greater role in sociopositive contexts, because their animals need to be especially attentive to social cues and signals emitted by conspecifics to achieve tolerance and close contact. This does by no means imply that social competence is restricted to sociopositive behaviour. Social competent behaviour is likewise shown in aggressive contexts, such as when obtaining or defending a resource by efficient and appropriate aggressive displays (Arnold & Taborsky, 2010; Taborsky et al., 2012), or even when losing a contest over a resource (Lehner et al., 2011).

Because of the lack of sufficient studies on social competence, Table 1 summarizes accounts of studies demonstrating a link between social *behaviours* and philopatry in social species. There is quite robust empirical and theoretical evidence that more sociable, more cooperative and less aggressive behavioural tendencies are accompanied by philopatry (Cote et al., 2010; Duckworth et al., 2018;

TABLE 1 Review of behavioural tendencies in social species

Species	Type of sociality	Which sex?	Sociopositive	Cooperation	Aggressive behaviour	Mechanism of inheritance	Reference
Ambrosia beetle, <i>Xylosandrus saxisenii</i>	cooperative breeder	f		+		genetic	Biedermann, 2012
Common eastern bumble bee, <i>Bombus impatiens</i>	cooperative breeder	f	+			?	Guerin, 2017
<i>Neolamprologus pulcher</i>	cooperative breeder	both	+	—		environmental (social environment)	Fischer et al., 2017; Antunes, Magda et al., 2021
<i>Neolamprologus multifasciatus</i>	group living	f			+		Schradin & Lamprecht, 2002
Red-cockaded woodpecker, <i>Picoides borealis</i>	cooperative breeder	m		+		genetic	Pasinelli et al., 2004
Western bluebird, <i>Sialia mexicana</i>	facultative cooperative breeder (territorial breeder)	m			—	genetic	Duckworth, 2008, Duckworth & Kruuk, 2009
	facultative cooperative breeder (territorial breeder)	m			—	environmental (maternal stress)	Duckworth et al., 2015, Potticary et al., 2020
	facultative cooperative breeder (helper)	m		+		?	Potticary et al., 2018
Superb starling, <i>Lamprolornis superbus</i>	cooperative breeder	m		+		?	Shah & Rubenstein, 2021
Carion crow, <i>Corvus c. corone</i>	biparental (central Europe), cooperative breeders (Spain)	both		+	(1 of 6 birds)	environmental (parental effects or conditional?)	Baglione et al., 2002
House mouse, <i>Mus m. musculus</i>	facultative communal breeder	m			—	genetic	Krackow, 2003
African striped mouse, <i>Rhabdomys pumilio</i>	facultatively group living, facultative cooperative breeder in reproductive season	both	—		—	no inheritance (conditional on current density)	Schoepf & Schradin, 2012
Naked mole rat, <i>Heterocephalus glaber</i>	cooperative breeder	m		+		?	O'Riain et al., 1996, Toor et al., 2020
	cooperative breeder	m			—	?	Toor et al., 2020
Damaraland mole rat, <i>Fukomys damarensis</i>	cooperative breeder	m		—		no inheritance (conditional on quality?)	Zöttl et al., 2016, Torrents-Tico et al., 2018
Yellow-bellied marmot, <i>Marmota flaviventris</i>	group living	f	+				Blumstein et al., 2009
Spotted hyena, <i>Crocuta crocuta</i>	group living	m		+		?	Holekamp & Smale, 1998
Rhesus macaque, <i>Macaca mulatta</i>	group living	m	+		—	genetic (SERT polymorphism)	Mehlman et al., 1995, Trefilov et al., 2000

Note: In columns, "Sociopositive" (affiliation, submission), "Cooperation" (helping behaviours) and "Aggressive behaviour" "+" refers to an increase and "—" to a decrease of this behaviour in the more philopatric individuals of a species (compared to more dispersive individuals). Grey shaded field: philopatric individuals are of a more amicable, cooperative and less aggressive behavioural types; white fields: opposite behavioural type.



Mullon et al., 2018) both in social and solitary species. Table 1 reviewing social and facultatively social species confirms this trend by and large, with a few exceptions: philopatric individuals of striped mice show rather less amicable (but also less aggressive) behaviour towards some classes of conspecifics (Schoepf & Schradin, 2012). Subordinate group members of the philopatric phenotype of the cichlid *N. pulcher* show less direct alloparental care, but instead, they show more submission per received aggression by breeders (Fischer et al., 2017; Table A).

In most of the social species listed in Table 1, philopatry goes along with reduced aggression. The opposite is the case, however, in hyenas and the cichlid *N. fasciatus*, in which higher aggression helps dominant individuals to stay at a territory, whereas less competitive individuals are dispersive. In *N. fasciatus*, this happens even though dispersers are not attacked more often by dominants compared to non-dispersers (Schradin & Lamprecht, 2002).

In one study, the link between social competence and philopatry has been shown directly. In a rearing experiment, *N. pulcher* broods were raised in two different social environments (Box 1). Later in life fish from these two rearing treatments exhibited persistently two divergent social phenotypes, a more socially competent, philopatric type and a less competent disperser type, which showed more alloparental care before dispersal (Fischer et al., 2017, Table A).

Most examples in Table 1 reflect variation in social behaviour and dispersive propensities only for one sex, either for males or for females of a given species. In vertebrates, dispersal is often sexually dimorphic, with males being the more dispersing sex in mammals and some fish, and females dispersing more often in birds. While these broad sexual dimorphisms in behaviour are probably genetically determined, the interesting variation in the links between social competence and dispersal tendencies, as well as its subtle fitness consequences, occurs intrasexually, and therefore, many of the studies referred to in Table 1 covered one sex only.

A link between dispersal propensity and social behaviour can be caused by genetic correlations, by environmental influences (e.g. developmental plasticity), or both. In the cooperatively breeding bark beetle *X. saxisenii*, selecting for dispersal age revealed a genetic correlation in adults between delayed dispersal and increased helping behaviour (Biedermann, 2012). In male western bluebirds, the positive correlation between dispersal and aggression is partly genetic (Duckworth & Kruuk, 2009) and partly induced by maternal effects mediated by the laying order of sexes within a clutch (Duckworth et al., 2015; Potticary et al., 2020). Finally, the social phenotypes can be solely induced by developmental plasticity as in the study on *N. pulcher*, where the genetic background of the fish was controlled for by brood splitting (Fischer et al., 2017).

In summary, most often philopatry is related to more socially tolerant or to cooperative behaviour in social species (Table 1). This suggests that also social competence and philopatry may be part of the same social phenotype, as it has been often assumed that social competence plays a greater role in sociopositive contexts (reviewed above). This seems plausible, because when individuals get into close proximity, they need to be especially attentive to social cues and

signals emitted by conspecifics to achieve tolerance. As pointed out above, however, social competence is certainly not restricted to sociopositive behaviour but pertains to all social behaviours and social decisions.

While the collected evidence thus far suggests a possible association of social competence and philopatry in animal societies, the question to which degree dispersal behaviour, in particular, prospecting behaviour and forming relationships with members of a new group (Jungwirth et al., 2015; Raihani et al., 2010; Young et al., 2005), requires social competence will be a fascinating topic for future research. Recent theoretical work suggests that social learning, which is one important mechanism that can give rise to social competence, may favour dispersal because it reduces local adaptation (Sapage et al., 2021). However, dispersing individuals usually either enter smaller, existing groups, like in babblers (Raihani et al., 2010) or form new small groups with other dispersers. These smaller groups have less potential for resource competition and conflicts, so that after dispersal selection on social competence will be relaxed.

One may ask whether relatedness to other group members would select for higher or lower social competence. Social competence facilitates social life and increases the benefits or lowers the costs of social encounters (Part 1), but there is no reason why relatedness *per se* should affect social competence or vice versa, why social competence would increase indirect benefits. Indirect benefits, but also kin competition, along with a suite of other environmental factors influencing reproductive and survival prospects inside or outside the natal territory, are important drivers of individual decisions about whether stay or leave, but these factors are not directly linked to social competence.

### 3.2 | Is dispersal heritable?

There is an unfortunate lack of quantitative genetic studies quantifying proportions of variance explained by genetic and environmental components of dispersal propensity. A notable exception is the study on western bluebirds that found a high, significant genetic heritability of dispersal (Duckworth & Kruuk, 2009) as well as maternal effects on dispersal (Duckworth et al., 2015). Also the above-mentioned selection experiment in the bark beetle *Xylosandrus saxisenii* is evidence of genetic heritability of dispersal (Biedermann, 2012).

Several studies estimated the genetically heritable component of dispersal propensity through parent-offspring regressions, both in social and solitary birds and mammals (Charmanier et al., 2011; Doligez & Pärt, 2008). In their review, Doligez and Pärt (2008) reported low to intermediate heritabilities of dispersal propensity in birds. However, when estimated from observational data of natural populations, these regressions are inherently limited in their ability to tease apart genetic inheritance from non-genetic effects of the parental environment (Kasper et al., 2017b). Thus, even though most reported heritabilities were rather low, slopes of parent-offspring regressions tend to overestimate the genetic heritability

component. In collared flycatchers (*Ficedula albicollis*) and great tits (*Parus major*), dispersal propensity was found to be consistent within life time (i.e. repeatable; reviewed in Doligez & Pärt, 2008). In three social species, positive parent-offspring regressions for other dispersal traits were reported. Sire-offspring regressions revealed an additive genetic component of dispersal age in male, but not female, red wolves (Sparkman et al., 2012) and in house mice (Krackow, 2003), yet sample sizes were small. Likewise, there were significant father-son regressions for natal dispersal distance in red-cockaded woodpeckers: correlations were high in males dispersing right away from the natal territory, whereas they were intermediate in males which served as brood care helpers first before dispersing; mother-daughter correlations were low but significant (Pasinelli et al., 2004).

A genetic polymorphism determining the dispersal age has been identified in rhesus macaque males: individuals that delayed dispersal carry the long variant of a serotonin transporter gene (SERT) either as homozygotes or heterozygotes, resulting in higher transcriptional activity of this gene as compared to the disperser morph, which carries the homozygote short allele of this gene (Trefilov et al., 2000).

Prenatal non-genetic inheritance of dispersal traits can be mediated by maternal variation of egg composition. For example, a higher transfer of maternal yolk androgens might result in a larger offspring dispersal distance as simulated by androgen addition to great tit eggs (Tschirren et al., 2007). In western bluebirds, multiple maternal stressors including limited access to nest boxes, cold snaps and a greater distance to kin at neighbouring territories resulted in an increase of maternal corticosterone baseline levels (Potticary et al., 2020). These stressors also caused mothers to produce more sons early in the laying order, which have a higher dispersal propensity. Also this effect is apparently caused by yolk androgens, which occur in higher concentrations in early-laid eggs (Duckworth et al., 2015).

An interesting experiment testing for postnatal environment-induced delayed dispersal was performed in carrion crows (*Corvus c. corone*). Hatchlings from pairs of a biparental Swiss population were transplanted into nests of cooperatively breeding Spanish crows; half of each experimental brood were retained in the original Swiss habitat as control. While the Swiss siblings left the natal territory soon after independence, their transplanted siblings in Spain delayed dispersal as did the native offspring from the Spanish population. One transplanted individual even joined alloparental care as helper at the nest (Baglione et al., 2002). In this particular study, delaying dispersal after being transplanted might be a developmentally plastic strategy when nestlings perceived cues by their foster parents or the environment that induced delayed dispersal and helping. Alternatively, it might represent a socially flexible response towards the lack of opportunity to occupy an own territory after fledging.

In summary, there is good evidence in several social species that the propensity to remain philopatric or to disperse is transmitted across generations, and this inheritance can have a genetic and/or environmental basis, even if both components together have been rarely studied.

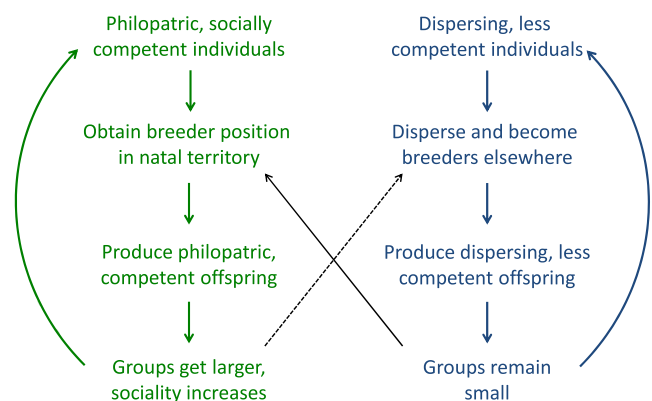
### 3.3 | Evolutionary consequences

Sections (a) and (b) of part 2 provide support that the preconditions for a positive feedback between sociality and social competence mediated by dispersal propensity are met. There is at least some evidence that high social competence and philopatry can be part of the same individual social phenotype, and that dispersal can be genetically and/or non-genetically transmitted across generations. Here, I discuss the potential consequences of the positive feedback (see Figure 2). Using cooperative breeders as example, philopatric, socially competent individuals may eventually obtain the position of a dominant breeder at their natal territory (see left side of Figure 2, green feedback). They will then transmit their social phenotype to offspring, which consequently will have a high propensity to remain philopatric. Thus, over time group sizes of this social phenotype as well as within-group competition will increase, eliciting stronger selection on even higher social competence. So over several generations, social competence and the level of sociality (in this simplified example represented by group size) will both increase.

At the right side of Figure 2 (blue feedback), the opposite happens: a dispersive individual with low social competence produces offspring that tend to disperse away from the natal territory; thereby, these social groups rather remain small, and there is no strong selection pressure on improved social competence.

What could be the evolutionary consequences of the two feedbacks depicted in Figure 2?

**Genetic polymorphism:** If social phenotypes, that is dispersal tendency and social competence, were predominantly genetically transmitted, disruptive selection could occur, leading to the evolution of a behavioural polymorphism. This polymorphism could be stabilized by negative frequency-dependent selection or by fluctuating environmental conditions, and result in a bimodal distribution of group sizes. If morphs would mate assortatively, gene flow between them



**FIGURE 2** Hypothetical mechanism of how sociality and social competence may co-evolve. Please refer to text for the explanations of green (left side) and blue (right side) feedback loops. Black, diagonal arrows become relevant when social competence and dispersal tendencies are developmentally plastic (see text)

would become more and more reduced, and ultimately large and small group populations might become separated.

However, to my knowledge, there are no published accounts of bimodal group-size distributions in social species within a population. In almost all published cases, group-size distributions are unimodal. Bimodality might be expected in facultative cooperative breeders. Here, the smaller mode has invariably a group size of two (a monogamous breeder pair) and the larger mode follows the distribution of helper numbers in addition to the two breeders. The only example that comes near such bimodal distribution is the campo flicker (*Colaptes c. campestris*), a facultative cooperative breeder, in which roughly 60% of groups are pairs (group size of two) and the other 40% are cooperative groups with a median size of four group members. Dispersal in these birds is rare, and it has been described only from the groups of the large group-size mode (groups with helpers) (Dias et al., 2013).

**Developmental plasticity:** If a social phenotype linking social competence and philopatry is induced by developmental plasticity, as in *N. pulcher* (see Box 1), the social phenotype can be transmitted non-genetically: young develop their social phenotype according to their social rearing condition (e.g. a large or a small group, Fischer et al., 2015). They themselves will live and reproduce in a similar social environment as they grew up in, and thereby their offspring will adopt a social phenotype resembling that of their parents (two feedbacks in Figure 2). In case of developmental plasticity, the two feedbacks will be interconnected, when a few individuals occasionally switch from small groups to large groups (diagonal solid arrow) or from large to small groups (diagonal dashed arrow). If that happens, offspring of “group-size switchers” grow up in a different social environment than their parents and will develop the opposite social phenotype than their parents have.

Switching between group sizes by dispersers happens often after a period of prospecting (meerkats, Young et al., 2005; pied babblers, Raihani et al., 2010; *N. pulcher*, Jungwirth et al., 2015). Field studies showed that in many social species fitness is considerable higher in large than in small groups (e.g. *N. pulcher*, Brouwer et al., 2005; apostlebirds, *Struthidea cinerea*, Woxvold & Magrath, 2005; pied babblers, Ridley, 2016; meerkats, *Suricata suricatta*, Groenewoud & Clutton-Brock, 2020). In these species, positions in large groups are highly competed for, so that switches from small to large groups may be challenging. For instance, *N. pulcher* adults, which successfully switch to larger groups, accomplish this mostly when they had been already a dominant breeder, albeit in small groups (Jungwirth et al., subm), whereas subordinates mostly disperse into same sizes or smaller groups. When existing groups are small, any additional group member reduces the workload for dominants or for all members and increases safety from predation (Brouwer et al., 2005; Groenewoud et al., 2016). Therefore, being accepted as subordinate can be much easier in small groups than in large groups (Ridley, 2016). Moving from larger to a smaller group may also be beneficial if the move shortens one's own position in the queue for a breeding position (Jungwirth et al., 2015) or if the costs of within-group competition for resources become too high. It may also happen if dispersers form a new breeder group, which

may initially consist only of a few animals dispersing together (Cant et al., 2010).

Occasional switches between group sizes by developmental plasticity should prevent the emergence of two group-size modes. This is in line with published accounts on group-size distributions, which are almost always unimodal. Typically, facultative cooperative breeders (red-cockaded woodpeckers, Walters & Garcia, 2016; western bluebirds, Dickinson & Akre, 1998, Potticary et al., 2018; white-browed sparrow weavers, *Plocepasser mahali*, Harrison et al., 2013; alpine marmots, *Marmota marmota*, Grimm et al., 2003), as well as cooperative breeders with few helpers (carrion crows, Baglione & Canestrari, 2016; grey-crowned babbler, *Pomatostomus temporalis*, Edwards & Kot, 1995) and communal breeders with small groups (greater ani, *Crotophaga major*, Riehl, 2021) have unimodal, right-skewed group-size distributions. Obligate cooperative breeders and communal breeders with large groups and tend to have unimodal, symmetrical group-size distributions (pied babblers, Ridley, 2016; grey-throated babbler, *Stachyris nigriceps*, Kaiser et al., 2018; guira cuckoos, *Guira guira*; Macedo, 2016, cichlids, *N. pulcher* Balshine et al., 2001).

## 4 | CONCLUSIONS

The social environment of animals influences individual social decisions, which in turn feeds back on the social environment. In their review, Cantor and colleagues (2020) pointed out that the two halves of this feedback loop are rarely studied in conjunction. The positive feedback between sociality and social competence proposed here is such a loop, which has not yet been systematically studied. Because social competence increases the performance during social encounters of all kinds, positive feedback between selection on social competence and sociality seems plausible. Here, I reviewed the available evidence for the existence of this feedback loop. I also highlighted the enormous gaps in our knowledge, in particular, on the functional significance of social competence, its heritability, and of its correlations to life history traits (such as dispersal). With this review, I hope to motivate research for a fuller understanding of social competence and its evolutionary consequences.

## ACKNOWLEDGEMENTS

This paper is dedicated to my husband Michael Taborsky, to thank him for the unconditional support I received from him from the very first days of my scientific life onwards through until today, and for him being the most inspiring and knowledgeable discussion partner I can imagine. BT acknowledges financial support by the Swiss National Science Foundation (SNSF, project 31003A\_179208). Open Access Funding provided by Universitat Bern.

## CONFLICT OF INTEREST

I declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

No original data are included.

## ORCID

Barbara Taborsky  <https://orcid.org/0000-0003-1690-8155>

## REFERENCES

- Adkins-Regan, E., & Krakauer, A. (2000). Removal of adult males from the rearing environment increases preference for same-sex partners in the zebra finch. *Animal Behaviour*, 60, 47–53. <https://doi.org/10.1006/anbe.2000.1448>.
- Antunes, D. F., Magda, C., Teles, M. C., Zuelling, M., Friesen, C. N., Oliveira, R. F., Aubin-Horth, N., & Taborsky, B. (2021). Early social deprivation shapes neuronal programming of the social decision-making network in a cooperatively breeding fish. *Molecular Ecology*, in press.
- Antunes, D. F., Reyes-Contreras, M., Glauser, G., & Taborsky, B. (2021). Early social experience has life-long effects on baseline but not stress-induced cortisol levels in a cooperatively breeding fish. *Hormones and Behavior*, 128, 104910. <https://doi.org/10.1016/j.yhbeh.2020.104910>.
- Antunes, D. F., & Taborsky, B. (2020). Early social and ecological experience triggers divergent reproductive investment strategies in a cooperative breeder. *Scientific Reports*, 10, 10407. <https://doi.org/10.1038/s41598-020-67294-x>.
- Arnold, C., & Taborsky, B. (2010). Social experience in early ontogeny has lasting effects on social skills in cooperatively breeding cichlids. *Animal Behaviour*, 79, 621–630. <https://doi.org/10.1016/j.anbehav.2009.12.008>.
- Baglione, V., & Canestrari, D. (2016). Carrion crows: Family living and helping in a flexible social system. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates* (pp. 97–114). Cambridge University Press.
- Baglione, V., Canestrari, D., Marcos, J. M., Griesser, M., & Ekman, J. (2002). History, environment and social behaviour: experimentally induced cooperative breeding in the carrion crow. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 269, 1247–1251. <https://doi.org/10.1098/rspb.2002.2016>.
- Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M., & Werner, N. (2001). Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology*, 50, 134–140. <https://doi.org/10.1007/s002650100343>.
- Bastian, M. L., Sponberg, A. C., Sponberg, A. C., Suomi, S. J., & Higley, J. D. (2003). Long-term effects of infant rearing condition on the acquisition of dominance rank in juvenile and adult rhesus macaques (*Macaca mulatta*). *Developmental Psychobiology*, 42, 44–51. <https://doi.org/10.1002/dev.10091>.
- Bergmüller, R., & Taborsky, M. (2005). Experimental manipulation of helping in a cooperative breeder: helpers 'pay to stay' by preemptive appeasement. *Animal Behaviour*, 69, 19–28. <https://doi.org/10.1016/j.anbehav.2004.05.009>.
- Biedermann, P. (2012). *Evolution of cooperation in ambrosia beetles*. PhD Thesis. University of Bern, Switzerland.
- Blumstein, D. T., Wey, T. W., & Tang, K. (2009). A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proceedings of the Royal Society B-Biological Sciences*, 276, 3007–3012. <https://doi.org/10.1098/rspb.2009.0703>.
- Bourke, A. (2011). *Principles of Social Evolution*. Oxford University Press.
- Branchi, I. (2009). The mouse communal nest: Investigating the epigenetic influences of the early social environment on brain and behavior development. *Neuroscience and Biobehavioral Reviews*, 33, 551–559. <https://doi.org/10.1016/j.neubiorev.2008.03.011>.
- Branchi, I., D'Andrea, I., Fiore, M., Di Fausto, V., Aloe, L., & Alleva, E. (2006). Early social enrichment shapes social behavior and nerve growth factor and brain-derived neurotrophic factor levels in the adult mouse brain. *Biological Psychiatry*, 60, 690–696. <https://doi.org/10.1016/j.biopsych.2006.01.005>.
- Brouwer, L., Heg, D., & Taborsky, M. (2005). Experimental evidence for helper effects in a cooperatively breeding cichlid. *Behavioral Ecology*, 16, 667–673. <https://doi.org/10.1093/beheco/ari042>.
- Bshary, R., & Oliveira, R. F. (2015). Cooperation in animals: toward a game theory within the framework of social competence. *Current Opinion in Behavioral Sciences*, 3, 31–37. <https://doi.org/10.1016/j.cobeha.2015.01.008>.
- Camerlink, I., Turner, S. P., Farish, M., & Arnott, G. (2019). Advantages of social skills for contest resolution. *Royal Society Open Science*, 6, 181456. <https://doi.org/10.1098/rsos.181456>.
- Cant, M. A., Hodge, S. J., Bell, M. B. V., Gilchrist, J. S., & Nichols, H. J. (2010). Reproductive control via eviction (but not the threat of eviction) in banded mongooses. *Proceedings of the Royal Society B-Biological Sciences*, 277, 2219–2226. <https://doi.org/10.1098/rspb.2009.2097>.
- Cantor, M., Maldonado-Chaparro, A. A., Beck, K. B., Brandl, H. B., Carter, G. G., He, P., Hillemann, F., Klarevas-Irby, J. A., Ogino, M., Papageorgiou, D., Prox, L., & Farine, D. R. (2020). The importance of individual-to-society feedbacks in animal ecology and evolution. *Journal of Animal Ecology*, 90(1), 27–44. <https://doi.org/10.1111/1365-2656.13336>.
- Charmantier, A., Buoro, M., Gimenez, O., & Weimerskirch, H. (2011). Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross. *Journal of Evolutionary Biology*, 24, 1487–1496. <https://doi.org/10.1111/j.1420-9101.2011.02281.x>.
- Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 4065–4076. <https://doi.org/10.1098/rstb.2010.0176>.
- Curley, J. P., Davidson, S., Bateson, P., & Champagne, F. A. (2009). Social enrichment during postnatal development induces transgenerational effects on emotional and reproductive behavior in mice. *Frontiers in Behavioral Neuroscience*, 3, 25. <https://doi.org/10.3389/neuro.08.025.2009>.
- DeWitt, T. J., Sih, A., & Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution*, 13, 77–81. [https://doi.org/10.1016/S0169-5347\(97\)01274-3](https://doi.org/10.1016/S0169-5347(97)01274-3).
- Dias, R. I., Macedo, R. H., Goedert, D., & Webster, M. S. (2013). Cooperative breeding in the campo flicker II: Patterns of reproduction and kinship. *Condor*, 115, 855–862. <https://doi.org/10.1525/cond.2013.120143>.
- Dickinson, J. L., & Akre, J. J. (1998). Extrapair paternity, inclusive fitness, and within-group benefits of helping in western bluebirds. *Molecular Ecology*, 7, 95–105. <https://doi.org/10.1046/j.1365-294x.1998.00320.x>.
- Doligez, B., & Part, T. (2008). Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *Journal of Animal Ecology*, 77, 1199–1211. <https://doi.org/10.1111/j.1365-2656.2008.01446.x>.
- Dolivo, V., & Taborsky, M. (2015). Cooperation among Norway rats: The importance of visual cues for reciprocal cooperation, and the role of coercion. *Ethology*, 121, 1071–1080. <https://doi.org/10.1111/eth.12421>.
- Doutrelant, C., McGregor, P. K., & Oliveira, R. F. (2001). The effect of an audience on intrasexual communication in male Siamese fighting fish, *Betta splendens*. *Behavioral Ecology*, 12, 283–286. <https://doi.org/10.1093/beheco/12.3.283>.
- Dreiss, A. N., Ruppli, C. A., Delarbre, A., Faller, C., & Roulin, A. (2017). Responsiveness to siblings' need increases with age in vocally negotiating barn owl nestlings. *Behavioral Ecology and Sociobiology*, 71, 109. <https://doi.org/10.1007/s00265-017-2342-0>.
- Duckworth, R. A. (2008). Adaptive dispersal strategies and the dynamics of a range expansion. *American Naturalist*, 172, S4–S17. <https://doi.org/10.1086/588289>.



- Duckworth, R. A., Belloni, V., & Anderson, S. R. (2015). Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. *Science*, 347, 875–877. <https://doi.org/10.1126/science.1260154>.
- Duckworth, R. A., & Kruuk, L. E. B. (2009). Evolution of genetic integration between dispersal and colonization ability in a bird. *Evolution*, 63, 968–977. <https://doi.org/10.1111/j.1558-5646.2009.00625.x>.
- Duckworth, R. A., Potticary, A. L., & Badyaev, A. V. (2018). On the origins of adaptive behavioral complexity: Developmental channeling of structural trade-offs. *Advances in the Study of Behavior*, 50, 1–36.
- Edwards, S. V., & Kot, M. (1995). Comparative methods at the species level: Geographic variation in morphology and group size in grey-crowned babblers (*Pomatostomus temporalis*). *Evolution*, 49, 1134–1146.
- Emlen, S. T. (1982). The evolution of helping. 1. An ecological constraints model. *American Naturalist*, 119, 29–39.
- Farooqi, S. H., & Koyama, N. F. (2016). The occurrence of postconflict skills in captive Immature chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, 37, 185–199. <https://doi.org/10.1007/s10764-016-9893-1>.
- Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., & Taborsky, B. (2015). Rearing group size determines social competence and brain structure in a cooperatively breeding cichlid. *American Naturalist*, 186, 123–140. <https://doi.org/10.1086/681636>.
- Fischer, S., Bohn, L., Oberhammer, E., Nyman, C., & Taborsky, B. (2017). Divergence of developmental trajectories is triggered interactively by early social and ecological experience in a cooperative breeder. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E9300–E9307. <https://doi.org/10.1073/pnas.1705934114>.
- Francis, D., Diorio, J., Liu, D., & Meaney, M. J. (1999). Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science*, 286, 1155–1158. <https://doi.org/10.1126/science.286.5442.1155>.
- Fuxjager, M. J., Montgomery, J. L., & Marler, C. A. (2011). Species differences in the winner effect disappear in response to post-victory testosterone manipulations. *Proceedings of the Royal Society B-Biological Sciences*, 278, 3497–3503. <https://doi.org/10.1098/rspb.2011.0301>.
- Gennuso, M. S., Brivido, M., Pave, R., Rano, M., & Kowalewski, M. (2018). Social play among black and gold howler monkey (*Alouatta caraya*) immatures during intergroup encounters. *American Journal of Primatology*, 80, e22909.
- Grantner, A., & Taborsky, M. (1998). The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces:Cichlidae). *Journal of Comparative Physiology B*, 168, 427–433. <https://doi.org/10.1007/s003600050162>.
- Grimm, V., Dorndorf, N., Frey-Roos, F., Wissel, C., Wyszomirski, T., & Arnold, W. (2003). Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*. *Oikos*, 102, 124–136.
- Groenewoud, F., & Clutton-Brock, T. (2020). Meerkat helpers buffer the detrimental effects of adverse environmental conditions on fecundity, growth and survival. *Journal of Animal Ecology*, 90(3), 641–652.
- Groenewoud, F., Frommen, J. G., Josi, D., Tanaka, H., Jungwirth, A., & Taborsky, M. (2016). Predation risk drives social complexity in cooperative breeders. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 4104–4109. <https://doi.org/10.1073/pnas.1524178113>.
- Groothuis, T. G. G., & Taborsky, B. (2015). Introducing biological realism into the study of developmental plasticity in behaviour. *Frontiers in Zoology*, 12(Suppl 1), S6. <https://doi.org/10.1186/1742-9994-12-S1-S6>.
- Guerin, C. (2017). *Idiosyncratic social behavior within bumble bee (Bombus impatiens) colonies impacts reproductive potential of workers*. MSc Thesis, Harvard University, USA.
- Harrison, X., York, J., Cram, D., Hares, M., & Young, A. (2013). Complete reproductive skew within white-browed sparrow weaver groups despite outbreeding opportunities for subordinates of both sexes. *Behavioral Ecology and Sociobiology*, 67, 1915–1929. <https://doi.org/10.1007/s00265-013-1599-1>.
- Heg, D., Bachar, Z., Brouwer, L., & Taborsky, M. (2004). Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society London, Series B*, 271, 2367–2374. <https://doi.org/10.1098/rspb.2004.2855>.
- Hesse, S., Anaya-Rojas, J. M., Frommen, J. G., & Timo Thünken, T. (2015). Social deprivation affects cooperative predator inspection in a cichlid fish. *Royal Society Open Science*, 2, 140451.
- Higley, J. D., King, S. T., Hasert, M. F., Champoux, M., Suomi, S. J., & Linnoila, M. (1996). Stability of interindividual differences in serotonin function and its relationship to severe aggression and competent social behavior in rhesus macaque females. *Neuropsychopharmacology*, 14, 67–76. [https://doi.org/10.1016/S0893-133X\(96\)80060-1](https://doi.org/10.1016/S0893-133X(96)80060-1).
- Holekamp, K. E., & Smale, L. (1998). Dispersal status influences hormones and behavior in the male spotted hyena. *Hormones and Behavior*, 33, 205–216. <https://doi.org/10.1006/hbeh.1998.1450>.
- Johnstone, R. (2001). Eavesdropping and animal conflict. *Proceedings of the National Academy of Sciences USA*, 98, 9177–9180.
- Jungwirth, A., Walker, J., & Taborsky, M. (2015). Prospecting precedes dispersal and increases survival chances in cooperatively breeding cichlids. *Animal Behaviour*, 106, 107–114. <https://doi.org/10.1016/j.anbehav.2015.05.005>.
- Jungwirth, A., Zöttl, M., Bonfils, D., Josi, D., Frommen, J. G., & Taborsky, M. (MS). *Benefits of philopatry and fitness effects of sex-specific life histories in a cooperative breeder*. Subm manuscript.
- Kaiser, S. A., Martin, T. E., Oteyza, J. C., Armstad, C., & Fleischer, R. C. (2018). Direct fitness benefits and kinship of social foraging groups in an Old World tropical babbler. *Behavioral Ecology*, 29, 468–478. <https://doi.org/10.1093/beheco/arx196>.
- Kasper, C., Kolliker, M., Postma, E., & Taborsky, B. (2017b). Consistent cooperation in a cichlid fish is caused by maternal and developmental effects rather than heritable genetic variation. *Proceedings of the Royal Society B-Biological Sciences*, 284, 20170369. <https://doi.org/10.1098/rspb.2017.0369>.
- Kasper, C., Schreier, T., & Taborsky, B. (2019). Heritabilities, social environment effects and genetic correlations of social behaviours in a cooperatively breeding vertebrate. *Journal of Evolutionary Biology*, 32, 955–973. <https://doi.org/10.1111/jeb.13494>.
- Kasper, C., Vierbuchen, M., Ernst, U., Fischer, S., Radersma, R., Raulo, A., Cunha-Saraiva, F., Wu, M., Mobley, K. B., & Taborsky, B. (2017a). Genetics and developmental biology of cooperation. *Molecular Ecology*, 26, 4364–4377. <https://doi.org/10.1111/mec.14208>.
- Kempes, M. M., Gulickx, M. M. C., van Daalen, H. J. C., Louwerse, A. L., & Sterck, E. H. M. (2008). Social competence is reduced in socially deprived rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 122, 62–67. <https://doi.org/10.1037/0735-7036.122.1.62>.
- Koenig, W. D., & Dickinson, J. L. (2016). *Cooperative breeding in vertebrates*. Cambridge University Press.
- Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, 358, 493–495. <https://doi.org/10.1038/358493a0>.
- Krackow, S. (2003). Motivational and heritable determinants of dispersal latency in wild male house mice (*Mus musculus musculus*). *Ethology*, 109, 671–689.
- Kralj-Fiser, S., Laskowski, K. L., & Garcia-Gonzalez, F. (2019). Sex differences in the genetic architecture of aggressiveness in a sexually



- dimorphic spider. *Ecology and Evolution*, 9, 10758–10766. <https://doi.org/10.1002/ece3.5595>.
- Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. *Journal of Evolutionary Biology*, 20, 1890–1903. <https://doi.org/10.1111/j.1420-9101.2007.01377.x>.
- Kuo, P. H., Lin, C. C. H., Yang, H. J., Soong, W. T., & Chen, W. J. (2004). A twin study of competence and behavioral/emotional problems among adolescents in Taiwan. *Behavior Genetics*, 34, 63–74. <https://doi.org/10.1023/B:BEGE.0000009477.70657.9d>.
- Laughlin, S. B., van Steveninck, R. R. D., & Anderson, J. C. (1998). A fundamental measure of the metabolic cost of neural information in the retina of the blowfly, *Calliphora vicina*. *Journal of Physiology-London*, 506P, 92P.
- Lehner, S. R., Rutte, C., & Taborsky, M. (2011). Rats benefit from winner and loser effects. *Ethology*, 117, 949–960. <https://doi.org/10.1111/j.1439-0310.2011.01962.x>.
- Leimar, O. (2021). The evolution of social dominance through reinforcement learning. *American Naturalist*, 197, 560–575. <https://doi.org/10.1086/713758>.
- Lerch, B. A., & Abbott, K. C. (2020). Allee effects drive the coevolution of cooperation and group size in high reproductive skew groups. *Behavioral Ecology*, 31, 661–671. <https://doi.org/10.1093/beheco/araa009>.
- Levy, F., Melo, A. I., Galef, G., Madden, M., & Fleming, A. S. (2003). Complete maternal deprivation affects social but not spatial learning in adult rats. *Developmental Psychobiology*, 43, 177–191. <https://doi.org/10.1002/dev.10131>.
- Lindholm, A. K., Hunt, J., & Brooks, R. (2006). Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae*. *Biology Letters*, 2, 586–589.
- Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., Sharma, S., Pearson, D., Plotsky, P. M., & Meaney, M. J. (1997). Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. *Science*, 277, 1659–1662. <https://doi.org/10.1126/science.277.5332.1659>.
- Macedo, R. (2016). Guira cuckoos: Cooperation, infanticide, and female reproductive investment in a joint-nesting species. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates* (pp. 257–271). Cambridge University Press.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge University Press.
- McGuire, S., Manke, B., Saudino, K. J., Reiss, D., Hetherington, E. M., & Plomin, R. (1999). Perceived competence and self-worth during adolescence: A longitudinal behavioral genetic study. *Child Development*, 70, 1283–1296. <https://doi.org/10.1111/1467-8624.00094>.
- Meaney, M. J., & Szyf, M. (2005). Maternal care as a model for experience-dependent chromatin plasticity? *Trends in Neurosciences*, 28, 456–463. <https://doi.org/10.1016/j.tins.2005.07.006>.
- Mehlman, P. T., Higley, J. D., Faucher, I., Lilly, A. A., Taub, D. M., Vickers, J., Suomi, S. J., & Linnoila, M. (1995). Correlation of CSF 5-HIAA concentration with sociality and the timing of emigration in free-ranging primates. *American Journal of Psychiatry*, 152, 907–913.
- Morrison, R. E., Eckardt, W., Stoinski, T. S., & Brent, L. J. N. (2020). Comparing measures of social complexity: larger mountain gorilla groups do not have a greater diversity of relationships. *Proceedings of the Royal Society B-Biological Sciences*, 287, 20201026. <https://doi.org/10.1098/rspb.2020.1026>.
- Mullon, C., Keller, L., & Lehmann, L. (2018). Social polymorphism is favoured by the co-evolution of dispersal with social behaviour. *Nature Ecology & Evolution*, 2, 132–140. <https://doi.org/10.1038/s41559-017-0397-y>.
- Nyman, C., Fischer, S., Aubin-Horth, N., & Taborsky, B. (2017). Effect of the early social environment on behavioural and genomic responses to a social challenge in a cooperatively breeding vertebrate. *Molecular Ecology*, 26, 3186–3203. <https://doi.org/10.1111/mec.14113>.
- Nyman, C., Fischer, S., Aubin-Horth, N., & Taborsky, B. (2018). Evolutionary conserved neural signature of early life stress affects animal social competence. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172344. <https://doi.org/10.1098/rspb.2017.2344>.
- Oliveira, R. F. (2009). Social behavior in context: Hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, 49, 423–440. <https://doi.org/10.1093/icb/icp055>.
- Oliveira, R. F., McGregor, P. K., & Latruffe, C. (1998). Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 265, 1045–1049. <https://doi.org/10.1098/rspb.1998.0397>.
- O'Riain, M. J., Jarvis, J. U. M., & Faulkes, C. G. (1996). A dispersive morph in the naked mole-rat. *Nature*, 380, 619–621. <https://doi.org/10.1038/380619a0>.
- Parent, C. I., Corp, D., Cameron, N. M., & Meaney, M. J. (2013). Maternal care associates with play dominance rank among adult female rats. *Developmental Psychobiology*, 55, 745–756.
- Pasinelli, G., Schiegg, K., & Walters, J. R. (2004). Genetic and environmental influences on natal dispersal distance in a resident bird species. *American Naturalist*, 164, 660–669. <https://doi.org/10.1086/424765>.
- Perry, A. C., Krakauer, A. H., McElreath, R., Harris, D. J., & Patricelli, G. L. (2019). Hidden Markov models reveal tactical adjustment of temporally clustered courtship displays in response to the behaviors of a robotic female. *American Naturalist*, 194, 1–16. <https://doi.org/10.1086/703518>.
- Pinto, A., Oates, J., Grutter, A., & Bshary, R. (2011). Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology*, 21, 1140–1144. <https://doi.org/10.1016/j.cub.2011.05.021>.
- Potticary, A. L., & Duckworth, R. A. (2018). Environmental mismatch results in emergence of cooperative behavior in a passerine bird. *Evolutionary Ecology*, 32, 215–229. <https://doi.org/10.1007/s10682-018-9933-8>.
- Potticary, A. L., & Duckworth, R. A. (2020). Multiple environmental stressors induce an adaptive maternal effect. *American Naturalist*, 196, 487–500. <https://doi.org/10.1086/710210>.
- Raihani, N. J., Nelson-Flower, M. J., Golabek, K. A., & Ridley, A. R. (2010). Routes to breeding in cooperatively breeding pied babblers *Turdoides bicolor*. *Journal of Avian Biology*, 41, 681–686. <https://doi.org/10.1111/j.1600-048X.2010.05211.x>.
- Ridley, A. R. (2016). Southern pied babblers: The dynamics of conflict and cooperation in a group-living society. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates* (pp. 115–132). Cambridge University Press.
- Riehl, C. (2021). Evolutionary origins of cooperative and communal nesting: lessons from the crotophagine cuckoos. *Ethology*, 127, 827–836.
- Roisman, G. I., & Fraley, R. C. (2012). A behavior-genetic study of the legacy of early caregiving experiences: Academic skills, social competence, and externalizing behavior in kindergarten. *Child Development*, 83, 728–742. <https://doi.org/10.1111/j.1467-8624.2011.01709.x>.
- Rosewarne, P. J., Wilson, J. M., & Svendsen, J. C. (2016). Measuring maximum and standard metabolic rates using intermittent-flow respirometry: a student laboratory investigation of aerobic metabolic scope and environmental hypoxia in aquatic breathers. *Journal of Fish Biology*, 88, 265–283. <https://doi.org/10.1111/jfb.12795>.
- Rutte, C., Taborsky, M., & Brinkhof, M. W. G. (2006). What sets the odds of winning and losing? *Trends in Ecology & Evolution*, 21, 16–21. <https://doi.org/10.1016/j.tree.2005.10.014>.
- Santostefano, F., Wilson, A. J., Niemela, P. T., & Dingemanse, N. J. (2017). Behavioural mediators of genetic life-history trade-offs: a test of

- the pace-of-life syndrome hypothesis in field crickets. *Proceedings of the Royal Society B-Biological Sciences*, 284, 20171567. <https://doi.org/10.1098/rspb.2017.1567>.
- Sapage, M., Varela, S. A. M., & Kokko, H. (2021). Social learning by mate-choice copying increases dispersal and reduces local adaptation. *Functional Ecology*, 35, 705–716. <https://doi.org/10.1111/1365-2435.13735>.
- Schank, J. C., Burghardt, G. M., & Pellis, S. M. (2018). Toward a theory of the evolution of fair play. *Frontiers in Psychology*, 9, 1167. <https://doi.org/10.3389/fpsyg.2018.01167>.
- Schausberger, P., Gratzner, M., & Strodl, M. A. (2017). Early social isolation impairs development, mate choice and grouping behaviour of predatory mites. *Animal Behaviour*, 127, 15–21. <https://doi.org/10.1016/j.anbehav.2017.02.024>.
- Schoepf, I., & Schradin, C. (2012). Differences in social behaviour between group-living and solitary African striped mice, *Rhabdomys pumilio*. *Animal Behaviour*, 84, 1159–1167. <https://doi.org/10.1016/j.anbehav.2012.08.019>.
- Schradin, C. (2013). Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 368, 20120346. <https://doi.org/10.1098/rstb.2012.0346>.
- Schradin, C., & Lamprecht, J. (2002). Causes of female emigration in the group-living cichlid fish *Neolamprologus multifasciatus*. *Ethology*, 108, 237–248.
- Schweinfurth, M. K., & Taborsky, M. (2018). Norway rats (*Rattus norvegicus*) communicate need, which elicits donation of food. *Journal of Comparative Psychology*, 132, 119–129. <https://doi.org/10.1037/com0000102>.
- Shah, S. S., & Rubenstein, D. R. (2021). Prenatal environmental variation, alternative reproductive tactics and the formation of a mixed-kin cooperative society. *bioRxiv*. <https://doi.org/10.1101/2021.02.10.430612>.
- Siracusa, E. R., Wilson, D. R., Studd, E. K., Boutin, S., Humphries, M. M., Dantzer, B., Lane, J. E., & Mcadam, A. G. (2019). North American red squirrels mitigate costs of territory defence through social plasticity. *Animal Behaviour*, 151, 29–42. <https://doi.org/10.1016/j.anbehav.2019.02.014>.
- Sparkman, A. M., Adams, J. R., Steury, T. D., Waits, L. P., & Murray, D. L. (2012). Evidence for a genetic basis for delayed dispersal in a cooperatively breeding canid. *Animal Behaviour*, 83, 1091–1098. <https://doi.org/10.1016/j.anbehav.2012.01.041>.
- Starrfelt, J., & Kokko, H. (2012). The theory of dispersal under multiple influences. In J. Clobert, M. Baguette, T. G. Benton, & J. M. Bullock (Eds.), *Dispersal ecology and evolution* (pp. 19–28). Oxford University Press.
- Taborsky, B. (2016a). Opening the black box of developmental experiments: Behavioural mechanisms underlying long-term effects of early social experience. *Ethology*, 122, 267–283.
- Taborsky, B. (2017). Developmental plasticity: Preparing for life in a complex world. In M. Naguib, J. Podos, L. Simmons, S. Barrett, S. D. Healy, & M. Zuk (Eds.), *Advances in the Study of Behavior* (pp. 49–99). Academic Press, Elsevier.
- Taborsky, B., Arnold, C., Junker, J., & Tschopp, A. (2012). The early social environment affects social competence in a cooperative breeder. *Animal Behaviour*, 83, 1067–1074. <https://doi.org/10.1016/j.anbehav.2012.01.037>.
- Taborsky, B., & Oliveira, R. F. (2012). Social competence: an evolutionary approach. *Trends in Ecology & Evolution*, 27, 679–688. <https://doi.org/10.1016/j.tree.2012.09.003>.
- Taborsky, B., Skubic, E., & Brintjes, R. (2007). Mothers adjust egg size to helper number in a cooperatively breeding cichlid. *Behavioral Ecology*, 18, 652–657. <https://doi.org/10.1093/beheco/arm026>.
- Taborsky, M. (2016b). Cichlid fishes: a model for the integrative study of social behavior. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding* (pp. 272–293). Cambridge Univ Press.
- Taborsky, M., Cant, M. A., & Komdeur, J. (2021). *The evolution of social behaviour*. Cambridge University Press. In 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. <https://doi.org/10.1098/rstb.2015.0084>.
- Tibbetts, E. A., Wong, E., & Bonello, S. (2020). Wasps use social eavesdropping to learn about individual rivals. *Current Biology*, 30, 3007–3010. <https://doi.org/10.1016/j.cub.2020.05.053>.
- Toor, I., Edwards, P. D., Kaka, N., Whitney, R., Ziolkowski, J., Monks, D. A., & Holmes, M. M. (2020). Aggression and motivation to disperse in eusocial naked mole-rats, *Heterocephalus glaber*. *Animal Behaviour*, 168, 45–58. <https://doi.org/10.1016/j.anbehav.2020.07.022>.
- Torrents-Tico, M., Bennett, N. C., Jarvis, J. U. M., & Zöttl, M. (2018). Growth affects dispersal success in social mole-rats, but not the duration of philopatry. *Biology Letters*, 14, 20180005. <https://doi.org/10.1098/rsbl.2018.0005>.
- Toth, M., Halasz, J., Mikics, E., Barsy, B., & Haller, J. (2008). Early social deprivation induces disturbed social communication and violent aggression in adulthood. *Behavioral Neuroscience*, 122, 849–854. <https://doi.org/10.1037/0735-7044.122.4.849>.
- Trefilov, A., Berard, J., Krawczak, M., & Schmidtke, J. (2000). Natal dispersal in rhesus macaques is related to serotonin transporter gene promoter variation. *Behavior Genetics*, 30, 295–301.
- Triki, Z., Emery, Y., Teles, M. C., Oliveira, R. F., & Bshary, R. (2020). Brain morphology predicts social intelligence in wild cleaner fish. *Nature Communications*, 11, 6423.
- Triki, Z., Wismer, S., Rey, O., Binning, S. A., Levorato, E., & Bshary, R. (2019). Biological market effects predict cleaner fish strategic sophistication. *Behavioral Ecology*, 30, 1548–1557. <https://doi.org/10.1093/beheco/arz111>.
- Tschirren, B., Fitze, P. S., & Richner, H. (2007). Maternal modulation of natal dispersal in a passerine bird: An adaptive strategy to cope with parasitism? *American Naturalist*, 169, 87–93. <https://doi.org/10.1086/509945>.
- Varela, S. A. M., Teles, M. C., & Oliveira, R. F. (2020). The correlated evolution of social competence and social cognition. *Functional Ecology*, 34, 332–343. <https://doi.org/10.1111/1365-2435.13416>.
- Walters, J. R., & Garcia, V. (2016). Red-cockaded woodpeckers: Alternative pathways to breeding success. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates* (pp. 58–76). Cambridge University Press.
- Weiss, B. M., & Foerster, K. (2013). Age and sex affect quantitative genetic parameters for dominance rank and aggression in free-living greylag geese. *Journal of Evolutionary Biology*, 26, 299–310. <https://doi.org/10.1111/jeb.12042>.
- White, D. J., Gersick, A. S., Freed-Brown, G., & Snyder-Mackler, N. (2010). The ontogeny of social skills: experimental increases in social complexity enhance reproductive success in adult cowbirds. *Animal Behaviour*, 79, 385–390. <https://doi.org/10.1016/j.anbehav.2009.11.014>.
- White, D. J., King, A. P., & West, M. J. (2002). Plasticity in adult development: Experience with young males enhances mating competence in adult male cowbirds, *Molothrus ater*. *Behaviour*, 139, 713–728. <https://doi.org/10.1163/156853902320262781>.
- Wismer, S., Pinto, A. I., Vail, A. L., Grutter, A. S., & Bshary, R. (2014). Variation in cleaner wrasse cooperation and cognition: Influence of the developmental environment? *Ethology*, 120, 519–531. <https://doi.org/10.1111/eth.12223>.
- Woxvold, I. A., & Magrath, M. J. L. (2005). Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. *Journal of Animal Ecology*, 74, 1039–1050. <https://doi.org/10.1111/j.1365-2656.2005.01001.x>.
- Young, A. J., Carlson, A. A., & Clutton-Brock, T. (2005). Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Animal Behaviour*, 70, 829–837. <https://doi.org/10.1016/j.anbehav.2005.01.019>.

Zöttl, M., Vullioud, P., Mendonca, R., Tico, M. T., Gaynor, D., Mitchell, A., & Clutton-Brock, T. (2016). Differences in cooperative behavior among Damaraland mole rats are consequences of an age-related polyethism. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 10382–10387. <https://doi.org/10.1073/pnas.1607885113>.

**How to cite this article:** Taborsky, B. (2021). A positive feedback loop between sociality and social competence. *Ethology*, 127, 774–789. <https://doi.org/10.1111/eth.13201>