



## INVITED PERSPECTIVES AND REVIEWS

# Opening the Black Box of Developmental Experiments: Behavioural Mechanisms Underlying Long-Term Effects of Early Social Experience

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**Abstract**

Typically, animals spend a considerable portion of their time with social interactions involving mates, offspring, competitors and group members. The social performance during these interactions can strongly depend on the social environment individuals have experienced early in life. Despite a considerable number of experiments investigating long-term effects of the early social environment, our understanding of the behavioural mechanisms mediating these effects is still limited, mainly for two reasons. (1) Only in few experimental studies have researchers actually observed and quantified the behaviour of their study animals *during* the social treatment. (2) Even if differences in social interactions between social rearing treatments are reported, these differences might not be *causally* linked to any observed long-term effects later in life. The aim of this review was to investigate whether behavioural records of animals during the experimental manipulation of their social environment can help (1) identifying behavioural mechanisms involved in a long-term effect and (2) obtaining a better understanding of the long-term consequences of early manipulations. First, I review studies that manipulated the social environment at an early stage of the ontogeny, observed the social interactions and behaviour *during* the social experience phase and subsequently tested the performance in social and non-social behavioural tasks at a later life stage. In all reviewed studies, treatment differences were reported both in social interactions during the social experience phase and in social and/or non-social behaviours later in life. Second, I discuss four classes of behavioural mechanisms that can cause the reported long-term effects of social experience, namely learning by experience, social learning, sensory stimulation and social cueing. I conclude that social interactions during the social experience phase should *always* be recorded for at least two reasons. Knowledge about how the social interactions differ between rearing treatments (1) permits researchers to formulate hypotheses about candidate mechanisms causing long-term effects on behaviour and (2) can help to interpret unexpected outcomes of developmental experiments. Finally, I propose that as a crucial ultimate step towards understanding effects of the early social environment, we should develop targeted experiments testing for the causality of identified candidate mechanism.

## Introduction

Developmental plasticity refers to the ability of individuals to alter their phenotypic development in response to environmental triggers perceived during ontogeny. It is a powerful mechanism allowing individuals to flexibly adapt to current or anticipated environmental conditions. Often developmental plasticity is irreversible (Piersma & Drent 2003; West-Eberhard 2003), and it should therefore only be selected for if phenotypic adjustments made early in life provide net fitness benefits over the entire life-span. The environmental-matching hypothesis proposes that developmental plasticity should maximize fitness in adult environmental conditions rather than at the time when the plastic adjustment is made (e.g. West-Eberhard 2003; Monaghan 2008). These future conditions can be anticipated by the developing organism through parental effects or own direct observations of the early environment (e.g. Uller 2008; Kasumovic 2013; Groothuis & Taborsky 2015). Such 'anticipatory plasticity' can only be beneficial if the future conditions can be reliably predicted (Fischer et al. 2011; Shea et al. 2011; Burgess & Marshall 2014). While the vast majority of developmental plasticity research to date has targeted morphological, physiological and life-history traits in plants and animals (West-Eberhard 2003), the interest in this field is now rapidly increasing also among behavioural biologists (for example, see special issue on behavioural plasticity; Foster 2013). Many animals spend a considerable portion of their time interacting socially either with mates, offspring, competitors or group members. It is therefore appropriate that many studies on behavioural development focus on the role of the early social environment in shaping the adult social behaviour (e.g. reviewed in Kasumovic & Brooks 2011; Taborsky & Oliveira 2012; Creel et al. 2013).

Nevertheless, our understanding of the *behavioural* mechanisms mediating long-term effects of the early social environment is surprisingly poor. We seem to know much more about gene networks or neuroendocrine pathways mediating effects of the social environment during development (see Champagne & Curley 2005; Meaney & Szyf 2005; Champagne 2010; Groothuis & Maestripieri 2013; Sachser et al. 2013; Taborsky & Taborsky 2015; for reviews) than we know about the role of social interactions experienced during early life that might trigger these effects. There are at least two important reasons for this gap in our knowledge. (1) There is a remarkable lack of experimental studies in which researchers actually observe and quantify the behaviour of their study animals

during the social treatment, so that social triggers inducing phenotypic effects will go unnoticed. (2) Even if social interactions during the social experience phase are recorded and if we detect systematic differences between the social treatments, we can never be sure whether these differences are indeed causally linked to the detected long-term effects on later performance or if they just covary with other, unmeasured causal factors. Experimental manipulations of suspected candidate behaviours, such as the simulation of the amount of tactile stimulation received by pups (Hellstrom et al. 2012) to explain the reprogramming of the stress axis in rats, are necessary to pin down the behavioural mechanisms.

In general, the possible behavioural mediators of early social environment effects can be broadly divided into two types. (1) Visual, chemical, acoustic or tactile cues providing information about key population parameters such as density, age and size structure or sex ratio. These are perceived by animals during their development and enable them to anticipate future conditions ('Social Cueing', see Kasumovic & Brooks 2011). Social cueing does not require social interactions. (2) Variation in early-life social interactions, such as variation in the quantity, quality and diversity of social interactions and relationships of individuals. Both types of social mediators can jointly influence the development of behaviour. Social cueing, such as olfactory information about the presence of same-sex conspecifics as predictor of future reproductive competition, will often provide sufficient information on prospects for future growth, survival and reproductive opportunities to allow making informed life-history allocation decisions (Kasumovic & Brooks 2011). Direct social interactions should be more important for fine-tuning the expression of appropriate social behaviour, and for acquiring social skills. Detailed information on the relative strength of an individual in relation to others within a population or the own position within a hierarchy can best be extracted during direct encounters with conspecifics. Moreover multiple and diverse interactions can help individuals to learn from experience how to respond adequately to social challenges and to acquire a better social competence (Taborsky & Oliveira 2012).

The use of social cues obtained at an early-life stage to predict the social conditions present at a later life stage ('socially cued anticipatory plasticity' or 'SCAP') has been recently comprehensively reviewed in the context of adult reproductive decisions (Kasumovic & Brooks 2011). Below, I briefly subsume the essence of this research. The main aim of this review was, however, to evaluate the role social interactions during

early ontogeny may play in the development of long-term differences of social behaviour in addition to 'remotely sensed' SCAP. By this, I aim to highlight the importance of behavioural observations conducted in developmental experiments not only after, but also *during* the phase when the study animals obtain their social experience. I refer only to experimental studies, as in observational studies it is almost impossible to distinguish between the many candidates of behavioural and ecological factors potentially responsible for an observed long-term effect. Remarkably few experimental studies manipulating the early social environment actually did report social behaviour and interactions during the treatment phase (Table 1). For obvious reasons, this review excludes the many developmental studies comparing socially reared animals with animals reared in isolation or by surrogate parents, or in which the social partner was temporally removed (reviewed in Kosten et al. 2012), as in these studies in at least one treatment no social interactions with conspecifics could occur. Studies in which one treatment consisted of handling by humans were excluded for the same reason.

### Social Cueing

Animals can assess certain characteristics of their social environment, such as sex ratio, density, availability of suitable mating partners or presence and strength of competitors without necessarily engaging in social interactions with conspecifics. They can do so simply by eavesdropping on cues emitted by conspecifics. For instance, density and sex ratio may be indicated by the frequencies of seeing, smelling or hearing conspecifics. Likewise, the quality of potential opponents or mates can be evaluated remotely if the latter produce reliable signals. For example, in crickets (*Tel Gryllus commodus*), calling rate is an honest signal of male quality that can be perceived and used by juveniles to assess the expected strength of intrasexual competition in the future (Bentsen et al. 2006). Such social cues obtained sufficiently early during ontogeny can bias development towards certain life-history trajectories. They can be adaptive, if the future social environment is predictable by the social cues. This form of plasticity, referred to as 'SCAP', has been recently reviewed in the context of mating strategies (Kasumovic & Brooks 2011). Most examples compiled in this review deal with terrestrial invertebrates, mainly in insects and spiders. As a general pattern, this review revealed that when social cues predict low adult intrasexual competition, males develop faster and mature earlier but smaller and lighter, whereas

the opposite suite of traits is expressed when cues of high-quality conspecifics are present during ontogeny. In contrast, females mature more quickly when during ontogeny cues predict that high-quality mates will be available.

Cues on the future social environment can already be obtained before birth through intrauterine position effects (Ryan & Vandenberg 2002) or through prenatal parental effects. Mothers can provide information to offspring on future environmental risk or resource shortage, either by depositing steroid hormones in the egg yolk (Groothuis & Schwabl 2008; McCormick 2009) or by providing them via the placental stream (Kaiser & Sachser 2005). However, the transmission of social information to offspring before birth does not necessarily reflect a maternal strategy to optimize offspring performance. If mothers are exposed to ambient social stressors and thus have higher fluctuating glucocorticoid levels they may signal own stress levels inadvertently to offspring, an effect that is mediated by the increased glucocorticoid levels of stressed mothers (reviewed in Love et al. 2013).

Experimental evidence suggests that the different life-history trajectories pursued in response to early-life social cues help offspring to cope with the specific environment predicted by these cues (environmental matching). In redback spiders (*Latrodectus hasselti*), larger males are superior competitors in direct contests with other males over access to female mating partners, which results in positive selection for male size. However, when reared in the presence of high female-densities, redback spider males matured faster and at smaller sizes than males growing up in high male densities (Kasumovic & Andrade 2009). Thus, the female-biased early sex ratio led to a reversal of the direction of sexual selection on male size. In subsequent mating performance tests, large males always performed better when directly competing with small males for females, whereas small males outperformed large males when given a 1-d head start before competition with large males sets in, that is, a condition simulating the faster development of small males (Kasumovic & Andrade 2009).

The expressed social behaviour can give rise to such context-dependent fitness differences in matching vs. non-matching environments, which can be shown by experiments exposing adult individuals reciprocally to each of two rearing conditions. For instance, zebra finch males were kept during adolescence (i.e. the experience phase) either in the company of a female (pair rearing), of another male, or of a group of males and females (group rearing), simulating an environ-

**Table 1:** Review of studies that manipulated the social environment during ontogeny, observed the social interactions in the treatment groups during the social experience phase, and tested for effects on social and non-social behaviours at a later life stage. If in column 'Social rearing treatment' one of the treatments is highlighted in italics, then the direction of the reviewed effects refer to this treatment

Species	Social rearing treatment	Life stage of manipulation	Social interactions during rearing	Affected life stage	Behavioural test	S or N	Effect on behaviour	References
<b>Quantity of social interactions</b>								
<i>Neolamprologus pulcher</i>	Adults and helper present or absent during first 2 mo of life	Dependent young	More peer-to-peer interactions	Juv	Competition for a resource (shelter)	S	More appropriate use of social behaviour by resource owner and intruders	Arnold & Taborsky (2010), Taborsky et al. (2012, 2013)
<i>Neolamprologus pulcher</i>	Large vs. small family groups	Dependent young	More peer-to-peer interactions	Ad	Integration in unfamiliar group	S	More submission towards dominant breeder pair	Fischer et al. (2015)
Laboratory mouse CD1	Communal vs. single-mother rearing	Dependent young	More maternal nest attendance and care (licking and nursing)	Juv	Hierarchy formation	S	More submission towards larger, dominant conspecific	Branchi et al. (2006)
Laboratory mouse CD1	Three age groups of pups (total birth spacing 7 d) under communal nesting (CN) and single-mother nesting (SN)	Dependent young	Old and young CN pups and SN pups received more maternal care (licking, AB nursing)	Ad males	Staged fight with unfamiliar male	S	Faster establishment of social hierarchy and expression of role typical behaviour (dominant or subordinate)	Branchi et al. (2013a)
Laboratory mouse CD1	Communal vs. single-mother rearing	Dependent young	All groups of CN pups had more peer-to-peer interactions	Ad males	Staged fight with unfamiliar male	S	More appropriate use of social behaviour during hierarchy establishment	Branchi et al. (2013b)
Laboratory mouse CD1	Communal vs. single-mother rearing	Dependent young	More received maternal care (licking, nursing) and more peer-to-peer interactions	Ad	Exposure to a dynamic group of 10 males (social stress)	S	More resilience to social stress	Branchi et al. (2013b)
Laboratory mouse CD1	Communal vs. single-mother rearing	Dependent young	More received maternal care (licking, nursing) and more peer-to-peer interactions (see Branchi et al. 2013b)	Ad	4 wk of daily 10-min swim (physical stress)	N	NO difference in vulnerability to physical stress	D'Andrea et al. (2007)
Laboratory mouse CD1	Communal vs. single-mother rearing	Dependent young	More received maternal care (licking, nursing) and more peer-to-peer interactions (see Branchi et al. 2013b)	Ad males	Hierarchy challenge (exchange of bedding material)	S	More aggressive behaviour	D'Andrea et al. (2007)

Table 1 (Continued)

Species	Social rearing treatment	Life stage of manipulation	Social interactions during rearing	Affected life stage	Behavioural test	S or N	Effect on behaviour	References
Laboratory mouse CD1	Communal vs. single-mother rearing	Dependent young	More received maternal care (licking, nursing) and more peer-peer interactions (see Branchi et al. 2013a,b)	Ad males	Water maze (spatial learning and memory) Induction of maternal behaviour by foreign pups	N	NO difference Less allomaternal care but more investigation of foreign pups	Gracceva et al. (2009)
Laboratory mouse CD1	CN with total birth spacing of 7, 5, or 3 d	Dependent young	The longer the birth spacing the more received maternal care and nest attendance	Ad males	Elevated zero maze Staged fight with unfamiliar male	N	NO difference 7 and 5 d spaced offspring more affiliative and investigative behaviour, 3d spaced offspring more aggression	Branchi et al. (2009)
Laboratory mouse Balb/c	Communal vs. single-mother rearing	Dependent young	More received maternal care (licking, nursing); less weight differences among pups	Ad females	Elevated plus maze Maternal behaviour under standard conditions Encounter with intruder male while caring for pups (7 d post-partum)	N	Shorter retrieval latency for own pups, more maternal care, better nest quality Lower aggression and more submission towards intruder males	Curley et al. (2009)
Sprague Dawley rat	Amount of maternal care towards old vs. young pups (4 d birth spacing) in a two-female communal nest	Dependent young	More maternal care	Subadult, Ad	Maternal behaviour under standard conditions Open field test Exposure to an unfamiliar conspecific matched for weight and age	S	More maternal care, larger litters Reduced anxiety-like behaviour in both generations Age-typical profile of social behaviours, which was not shown in second-born pups	Macri et al. (2010)

Table 1 (Continued)

Species	Social rearing treatment	Life stage of manipulation	Social interactions during rearing	Affected life stage	Behavioural test	S or N	Effect on behaviour	References
Mandarin vole, <i>Microtus mandarinus</i>	Biparental or maternal care	Dependent young	More overall care (huddling, licking) and more maternal care (lactating, licking)	Subadult, Ad	Elevated plus maze Locomotor activity in a novel environment Exposure to an unfamiliar conspecific matched for sex, size and age Exposure to an unfamiliar conspecific matched for sex, size and age Open field	N N S S N	Reduced anxiety NO difference in activity More self-grooming and general activity More body contact, dominance displays and general activity More locomotor activity, less anxious behaviour	Jia et al. (2009)
Quality of social interactions								
Bobwhite quail, <i>Colinus virginianus</i>	Contingent vs. non-contingent stimuli (using dummy and playback)	Dependent young	Maternal vocalization given contingently in response to distress calls of chicks	Dependent young	Filial imprinting to own species	S	Stronger imprinting	Harshaw & Lickliter (2007)
Laboratory rat (Long evans), <i>Rattus norvegicus</i>	High or low LG-ABN mothers (natural variation, experimentally validated by cross-fostering)	Dependent young	More licking and grooming (LG) and of arched-back nursing (ABN) received	Ad females	Rearing own pups	S	More LG and ABN towards own young	Liu et al. (1997), Francis et al. (1999)
Laboratory rat (Long evans), <i>Rattus norvegicus</i>	High or low LG-ABN mothers (natural variation, experimentally validated by cross-fostering)	Dependent young	More licking and grooming (LG) and of arched-back nursing (ABN) received	Ad	10-min open field test Morris water maze (spatial learning and memory)	N N	Reduced anxiety Better performance	Liu et al. (2000)
Laboratory rat (Long evans), <i>Rattus norvegicus</i>	High or low LG-ABN mothers (natural variation)	Dependent young	More licking and grooming (LG) received	Juv males	Dominance in social play (groups of 8)	S	Lower play dominance	Parent & Meaney (2008)
Laboratory rat (Long evans), <i>Rattus norvegicus</i>	High, mid or low LG-ABN mothers (natural variation)	Dependent young	More licking and grooming (LG) received	Ad females	Dominance in social play (groups of 3)	S	Lowest play dominance	Parent et al. (2013)

Table 1 (Continued)

Species	Social rearing treatment	Life stage of manipulation	Social interactions during rearing	Affected life stage	Behavioural test	S or N	Effect on behaviour	References
Rhesus macaques, <i>Macaca mulatta</i>	Normal vs. abusive maternal care (experimentally validated by cross-fostering)	Dependent young	More rejections and abusive behaviour received	Subadult and Ad females	Unmanipulated social groups during first 3 yrs of life	S	Stronger interest in infants of other females; NO difference in age at first conception	Maestriperi (2005a, b)
Diversity of social interactions								
Wolf spider, <i>Schizocosa uetzi</i>	Frequency of exposure to courting males	Subadult females	Frequency of contacts to courting males experimentally varied between 1 and 9 times	Ad females	Choice between two experimentally manipulated male phenotypes that can be familiar or unfamiliar	S	Stronger imprinting to familiar male phenotype if exposed more often to it during subadult stage	Hebets (2003)
Guppy, <i>Poecilia reticulata</i>	Adult conspecifics to simulate predator presence: <i>physical experience vs. only olfactory and visual experience vs. complete absence of adults</i>	Early juv stage	Direct agonistic and competitive interactions occurred between adults and juveniles	Juv	Shoaling test	S	NO general difference in shoaling tendency	Chapman et al. (2008a)
Redback salamander, <i>Plethodon cinereus</i>	2 adult males added from a <i>territorial vs. a non-territorial</i> population	Juv from non-territorial population	Competition with adult males for a shelter	Juv	Response to simulated avian predator attack	N	Faster response latency and longer escape distance	Liebigold (2014)
Zebra finch, <i>Taeniopygia guttata</i>	<i>With vs. without</i> males present in breeding colony	Dependent young	Paternal care and interactions with adult males occur	Ad males and females	Change of juvenile–juvenile encounters after experience with adults Two-choice preference test between male and female Test for pairing up in a group	S	Investigatory and escape behaviour increased after experience with territorial males and decreased after experience with non-territorial males NO behavioural differences Prefer opposite sex over same sex Higher pairing success	Adkins-Regan & Krakauer (2000)

**Table 1** (Continued)

Species	Social rearing treatment	Life stage of manipulation	Social interactions during rearing	Affected life stage	Behavioural test	S or N	Effect on behaviour	References
Brown cowbirds, <i>Molothrus ater</i>	Dynamic (exchange of group members) vs. static flock	Ad males	Developed larger, more variable 'singing network' with other males	Ad males	Direct competition between treatments for unfamiliar females	S	Higher copulation success	White et al. (2010)
Brown cowbirds, <i>Molothrus ater</i>	Flocks of adult males and juvenile and adult females with or without juvenile males	Ad males	Similar singing and mating behaviour, but less male-female associations before breeding season	Ad males	Direct competition between treatments for unfamiliar females	S	Higher copulation success; more singing behaviour	White et al. (2002a)
Brown cowbirds, <i>Molothrus ater</i>	Flocks of juvenile males and females with or without adult males	Juv	More intrasexual aggression, conspecific associations, natural courtship and copulation patterns, but song developed more slowly and has lower potency	Subadult males	Direct competition between treatments for unfamiliar females	S	NO difference in overall copulation success; lower copulation success per song towards female	White et al. (2002b)
Laboratory mouse CD1	Mixed sex (3:3) vs. female-only litters	Dependent young	More exploration, less social play	Ad females	Defence against males during pup rearing	S	More defence against males	Laviola & Terranova (1998)
House mouse, <i>Mus musculus</i> selected for long attack latency	Male pups reared with 5 male (single sex) or 5 female (mixed sex) pups	Dependent young (males)	More received maternal care, but less peer-to-peer interactions	Ad females	Pups removed from nest	S	Shorter latency to retrieve 1st pup	Benus & Henkelmann (1998)
				Ad females	Light-dark test, novel object test	N	Less fearful, more explorative	
Oldfield mouse, <i>Peromyscus polionotus</i>	With vs. without younger sibling pups	Subadult females	Access to pups prior to own reproduction	Ad males	Attack latency towards unfamiliar albino mouse	S	NO effect on attack latency	Margulis et al. (2005)
				Pups	Open field test	N	Less active	
				Ad males	Novel object test	N	Less neophobic	
				Ad males	Open field test	N	Less active	
				Ad males	Reversal learning in a Y maze	N	Poorer performance	
				Ad	Rearing own pups	S	Better nest quality	

Ad, Adults; Juv, Juveniles; S, social; N, non-social.

ment with a very low vs. a high density (Ruploh et al. 2013, 2014). After reaching adulthood, when confronted with a single unfamiliar female, pair-reared males were more aggressive towards other males, and they were more attractive for females than group-reared individuals (Ruploh et al. 2013). Conversely, when an adult male was placed in a larger mixed-sex group of unfamiliar zebra finches, group-reared males had an advantage as they integrated better in the group. No treatment differences in courtship and aggressive behaviour were present in the group setting (Ruploh et al. 2014). The effects on social behaviour reported in this study may have been caused by perceived cues of the population composition, such as population density, the number of same-sex competitors and/or the number of available mating partners. Alternatively, the effects may have been induced by a higher number of social interactions, a larger social interaction network or more diverse social interactions experienced when reared in groups compared to the pair-reared condition. As behavioural observations during the social rearing treatment are lacking, these alternatives cannot be distinguished. In the main part of this review, I will focus on studies in which behavioural records of focal animals during the social experience treatments are available.

### Manipulating the Nature of Social Interactions

Developmental experiments that manipulate the early social environment typically alter the level of social complexity, where a *higher* social complexity is defined here as a *greater quantity*, a *higher quality* or a *greater diversity* of encountered social interactions. Thus, a higher social complexity during development always involves some form of social enrichment. Typical sources of higher social complexity include the quantity and quality of parental care (Bateson 1994), group size and the diversity of group members (e.g. groups contain different social hierarchy levels, sexes, populations or age classes).

In general, social complexity can be manipulated in two ways, (1) by an unspecific manipulation, for example by generating environments generally allowing for *more* or *more intensive* social interactions of a certain type, such as mother-offspring interactions or interactions between siblings (peer-to-peer interactions), or (2) by specific manipulations of the composition of social groups that lead to a *greater diversity* of possible interactions, such as by adding types of social partners that are absent in the respective control treatments (e.g. rearing in mixed- vs. single-sex litters).

The research questions tackled by experiments varying the social environment broadly reflect the divide between unspecific and specific manipulations as outlined above. (1) Unspecific manipulations of social complexity serve to search for *any* kind of early environment effects, and typically, they test for a broad array of long-term effects on social behaviour, emotions and/or cognitive abilities (e.g. Graceveva et al. 2009). (2) Studies manipulating the composition of rearing groups often start with a specific hypothesis about the expected effect of their manipulations and only test for this particular effect later in life. Below and in Table 1, I summarize the main findings of studies performing unspecific or specific manipulations of social complexity. Remarkably, there seems to be a taxonomic bias in the way how early social experience is considered to affect later social behaviour and life-history decisions. While social cueing without direct social interactions has been considered predominantly in invertebrate species (see above), experiments reporting treatment effects of manipulated social interactions *during* the social experience phase appear to be done almost exclusively in vertebrates. Although there are notable exceptions, such as a study on colony-level aggressiveness experienced during larval stage on adult individual aggressiveness of honey bees (Rittschof et al. 2015), these studies did not report the interactions during the experience phase and thus cannot infer underlying mechanisms. Therefore, Table 1 exhibits an obvious taxonomic bias towards examples of mammals, birds and fish. Whether this bias reflects a tendency to study early social interactions preferentially in vertebrate species or if they play a minor role in the development of invertebrate social behaviour warrants further investigation.

### Quantity of Social Interactions

Long-term alterations of social behaviour in response to the observed quantity of social interactions have been particularly intensively studied in two model systems: *Nelamprologus pulcher*, a cooperatively breeding cichlid fish from Lake Tanganyika, and communally breeding laboratory strains of house mice, *Mus musculus*.

*Nelamprologus pulcher* breed in social groups of three to 25 members structured by a linear, size-dependent dominance hierarchy. Related and unrelated subordinate individuals help a dominant breeder pair rear their offspring. Several experiments tested for effects of varying social complexity of the rearing environment on the development of social competence (Arnold & Taborsky 2010; Taborsky et al. 2012;

Fischer et al. 2015). Social complexity was manipulated by either rearing the fish in groups without (young siblings only) or with age structure (parents, helpers and young siblings), or in small (parents plus one helper) vs. large groups (parents plus many helpers). Behavioural recordings during the social experience phase revealed that these manipulations caused an increase of the quantity of peer-to-peer interactions (Arnold & Taborsky 2010; Fischer et al. 2015). In contrast, direct interactions between young and older group members were not observed and thus cannot explain long-term effects on social behaviour (Arnold & Taborsky 2010). A series of different social challenge tests after the end of the social experience in juvenile and adult fish revealed that fish reared in the social environment with higher complexity were better able to cope with social conflicts and had a better outcome of social encounters (Table 1), that is, they had achieved a better social competence (Taborsky & Oliveira 2012).

The quantity of interactions has also been varied in laboratory mice, by rearing pups either with a single mother or in communal nests. Communal breeding, where several females jointly rear their pups in a common nest, increases social complexity in a number of different ways (Table 1): by increasing the amount of mother–infant contacts, the time young are attended by adults in the nest, the number of peer-to-peer interactions and the presence of peers of different ages as not all litters are produced simultaneously. It is difficult to disentangle which of these factors affect behavioural traits in pups. Correlation analyses suggest, however, that more mother–infant interactions favour more appropriate behaviour of offspring later in life during social hierarchy contests. In contrast, a higher amount of peer-to-peer interactions correlated positively with the expression of more affiliative behaviour *after* the social hierarchy was settled (Branchi et al. 2013a). Overall, communally reared male and female mice tended to display better social skills in an array of challenge tests, and females were better brood carers. One study found reduced maternal care by communally reared females, however (Gracceva et al. 2009), but this study investigated ‘maternal’ care for foreign pups only. Observations on interactions during the rearing phase comparing communally and singly nursing females to date only exist from laboratory strains of mice (Table 1), but not from wild-type house mice under natural conditions. Thus, it is as yet unknown whether the highly elevated numbers of social interactions observed in communal mice groups kept in the laboratory reflect the social conditions occurring in the wild.

### Quality of Social Interactions

While the above examples focussed on effects of interaction frequency, it is likely that the quality or intensity of social interactions can also exert strong and lasting influences on social behaviour. This is particularly expected when certain individuals repeatedly interact and thus build up social relationships (Weaver et al. 2004). For example, there is considerable natural variation in the quality of nursing and tactile pup stimulation in rodent mothers, which is independent of the total time they have direct contact to their pups (Meaney 2001). The so-called arched-back nursing (ABN) requires an active and most likely energy-consuming maintenance of a bent body position of the mother, which allows full and flexible access of pups to nipples. More relaxed nursing positions are less favourable for the pups. In rats, mothers performing more ABN also lick and groom (LG) their pups more often. Offspring of mothers providing high-quality maternal care, also referred to as ‘high LG-ABN’ mothers, express a lifelong reduced stress reactivity as compared to offspring from ‘low LG-ABN’ mothers. Most importantly, when adult they become high LG-ABN mothers themselves, thereby transmitting the environmental effect of their own early care experience to the next generation (Francis et al. 1999; Champagne & Meaney 2007). Cross-fostering experiments between high and low LG-ABN females showed that the long-term effects of care quality are induced by the pups’ environmental experience during their first 8 d of life. The long-term alterations in physiology and behaviour are induced and maintained by epigenetic reprogramming of the hypothalamic–pituitary–adrenal (HPA) axis (Meaney & Szyf 2005).

Natural variation in the quality of mother–infant relationships can influence later social behaviour also in primates. In rhesus monkey, some mothers show particularly poor care or even ‘abusive’ behaviour towards offspring: they frequently reject contacts by infants, or they even drop them or step on them. Female monkeys that had been exposed to abusive maternal care when young developed a significantly stronger interest in infants of other females during the juvenile stage than did monkeys reared by normally behaving mothers. This may indicate an advancement of pubertal behaviour (Maestripieri 2005a), although maternal care quality did not influence age at first conception. Cross-fostering experiments confirmed that the stronger interest in infants was environmentally induced by the poor maternal care quality. Like the rat study outlined above, the differences in mater-

nal care behaviour were transmitted to the next generation, as abusively treated females tended to become abusive mothers themselves (Maestripiere 2005b).

The most straightforward approach to explore the role of social interaction quality would be an experimental manipulation of the social interactions. This has been carried out only rarely. A notable exception is a study in Bobwhite quail manipulating the responsive behaviour of mothers towards signals of need by offspring, using behaving dummies. Quail mother dummies vocalizing towards chicks in response to the latter's distress calls induced stronger filial imprinting in chicks than did dummies producing identical calls at the same rate that were emitted randomly (Harshaw & Lickliter 2007), indicating that not only quantity and quality of social behaviour matters for long-term developmental effects, but also the behaviour must also be shown in the right context.

#### Diversity of Interactions

To manipulate the diversity of early social interactions, focal individuals are typically exposed to types of social partners that are absent in the respective control treatments. Exposure to, for instance, social partners of the opposite sex, different age classes, different breeding strains or populations creates opportunities for a more diverse array of social interactions than is available in socially more homogeneous rearing environments. Adding a specific type of social partners experimentally allows developing and testing specific hypotheses about the expected effects of these manipulations. For example, zebra finches reared in the presence of both adult females and males were expected to differentiate better between sexes as adults than birds reared with adult females only. Indeed, both male and female offspring of mixed-sex colonies expressed a stronger preference for opposite sex mating partners during adulthood than did finches reared in single-sex colonies (Adkins-Regan & Krakauer 2000).

A frequent manipulation to increase the diversity of interactions involves rearing young in either single-sex or mixed-sex litters (Benus & Henkelmann 1998; Laviola & Terranova 1998). During the social experience phase, mice reared in mixed-sex litters expressed a higher explorative tendency, received more maternal care but had less contacts with their litter mates (Table 1). After the experience phase, mice from mixed-sex litters were more aggressive towards unfamiliar mice (except adult males, Benus & Henkelmann 1998) and females showed shorter latencies to

retrieve pups that had been removed from the nest (Table 1).

Another way to enrich the social environment is to manipulate the age structure of groups. In cowbirds (*Molothrus ater*), the effects of mixed vs. single age classes were tested both in adult and in juvenile birds. Adult birds placed in mixed-age groups showed more courtship and mating related activities during the experience phase, while in juveniles, this treatment mainly affected courtship and song patterns. It was predicted that the mixed-age conditions will improve the later-life performance of males when directly competing for female mating partners. This hypothesis was confirmed only for males that got the social experience when they were already sexually mature, while a lower performance in this situation was observed in males that had been exposed to mixed-age flocks as juveniles (White et al. 2002a,b, 2010). A similar hypothesis was tested in guppies, where it had been predicted that the presence of adult males and females during rearing would increase the competence to obtain matings later in life. However, no effect of group composition was detected on mating behaviour and success (Magellan & Magurran 2009). Interestingly, another study in guppies used adult conspecifics to simulate predation risk to larvae and fry (Chapman et al. 2008a), although the adult guppies might as well also have been part of the social environment. Fish exposed to adults developed better escape abilities, but their shoaling tendency was unaffected.

#### Effects of Social Complexity on Non-Social Behaviour

The manipulation of social interactions during ontogeny can also affect non-social behaviours, including general activity, anxiety induced behaviour, explorative tendencies and spatial learning ability (Table 1). Interestingly, different forms of social enrichment can induce different directions of outcomes regarding these behaviours. While communally reared mice were more resilient to *social* stress, they did not differ from single-mother reared pups in their response to *physical* stress, anxiety level or spatial learning performance (Branchi et al. 2013b). In contrast, in rats, a higher amount (Macri et al. 2010) and a higher quality (Liu et al. 2000) of received maternal care was related to reduced anxiety and to a better spatial learning performance later in life. Also in mice, being reared in mixed-sex litters resulted in reduced anxiety and neophobia and higher explorativeness compared to mice from single-sex litters (Benus & Henkelmann 1998).

### Long-Term Behavioural Effects Induced by the Early Social Environment

Table 1 reviews the results of 52 social and non-social behavioural challenge tests done after an experimental variation of early social experience. In 92% of the 36 social challenge tests, the social performance later in life was affected by early experience. Of these effects, 64% revealed that the opportunities for more, better, or more diverse social experiences *increased* the performance in social tasks later in life. This suggests that enhancing social complexity early in life has improved the social skills in the majority of cases. In the other 36%, either there was no change in social performance or the direction of the effect (positive or negative) is difficult to evaluate from the information provided in the respective studies. Early social experience also affected the behaviour in non-social tasks in 75% of the challenge tests. When interpreting these figures, one has to take into account a potential publication bias towards studies that did find effects. Nevertheless, the figures impressively demonstrate the importance of early social environment for the development of social behaviour.

Animals reared in different early social environments and tested in multiple tasks later in life, such as *N. pulcher* and laboratory mice (see Table 1), showed effects of rearing on multiple social behaviours in multiple social contexts. This suggests the existence of a general mechanism acting on the entire social domain during development, resulting in a better *general* ability to flexibly cope with social challenges (i.e. social competence, Taborsky & Oliveira 2012). Possessing a better social competence should generally be beneficial in all kinds of social encounters across species. The expected benefits of social competence are expected to be particularly strong in highly social species, however, where virtually all behaviours involved in vital functions such as acquiring and defending resources, predator evasion and rearing offspring usually involve social interactions (Taborsky & Oliveira 2012). One possible, very general candidate mechanism that seems to be involved in the development of social competence is the reactivity of the vertebrate hormonal stress axis (HPA and HPI axes). Studies in mammals, birds and fish showed that the variation of early social complexity affects the expression of genes involved in the stress axis, with a key role taken by the expression of glucocorticoid receptors (GR, GR1) and the corticotropin-releasing factor (Meaney & Szyf 2005; Banerjee et al. 2012; Taborsky et al. 2013). HPA reactivity is also central to the adjustment of social behaviour to the social environ-

ment experienced in the adolescent phase in small rodents (Sachser et al. 2013). Interestingly, all but one of the non-social tasks reviewed in Table 1 investigating anxiety or neophobia reported a *reduction* of these traits after being reared in a more complex early social environment. Together with the finding that more socially complex conditions also increased the performance in social tasks in the majority of the cases, this suggests that a reduced anxiety and stress responsiveness may facilitate the expression of appropriate social behaviour and the acquisition of better social skills. The conclusions drawn from the studies compiled in Table 1 should be treated as a working hypotheses only. To test this hypothesis, formal statistical analysis following an exhaustive literature search would be required.

### The Value of Observing Behaviour During Rearing

This review has aimed to check whether obtaining behavioural records of animals *during* experimental exposure to different social experiences in their ontogeny helps to understand which behavioural mechanisms cause long-term behavioural effects later in life. The first and most obvious result of all available studies (Table 1) is that the social interactions between the focal individuals and their group mates differed between treatments already during the phase at which experimental individuals received the experience. This suggests that some or even most of the long-term effects may be causally related to treatment differences in the interactions focal animals experienced early in life, either directly (e.g. by training and learning), or indirectly because the different interactions trigger divergence in brain development. Apparently, the benefits of recording behavioural differences during the experience phase are at least two-fold. First, we can generate testable hypotheses about behavioural mechanisms underlying long-term effects of social experience, an aspect that is thus far little understood. Second, we may be able to explain eventual unexpected outcomes of experimental manipulations, as they may affect the interactions during the experience phase in ways not foreseen by the experimenter.

### Possible Behavioural Mechanisms

1 *Learning by experience.* If early contact to a particular class of social partners correlates with a better performance during interactions within the same social context later in life, it is obvious to assume that learning by experience occurred during early life. In Oldfield

mice (*Peromyscus polionotis*), for instance, the contact with pups in the subadult stage seems to enable them to build higher quality nests at the adult stage (Margulis et al. 2005). Experience in one social context can also help to learn the expression of adequate social behaviour in different future social contexts. *N. pulcher* offspring that had more social interactions with their siblings early in life performed better in tasks testing their performance in different social contexts, such as resource defence, integration in a group, and hierarchy formation (Arnold & Taborsky 2010; Taborsky et al. 2012; Fischer et al. 2015). In communally reared laboratory mice the frequency of interactions with other pups was positively related to the amount of affiliative behaviour shown after social hierarchies were established (Branchi et al. 2013a). Thus, frequent social interactions may provide a form of training that helps animals to cope with different social situations.

**2 Social learning.** Young animals may also acquire social skills by learning from other group members. In some of the reviewed studies referred to here, social learning may have taken place. However, social learning was not explicitly evident from any of the reported observations, and none of these studies has tested for this possibility. A study of guppies has proposed, however, that higher densities during rearing may increase the propensity to learn socially (Chapman et al. 2008b).

**3 Sensory stimulation.** Sensory stimulation by a social partner can modulate the quality of social interactions and/or it can act as a social cue. For example, tactile stimulation is important for a lower stress responsiveness in a number of rodents (Champagne & Meaney 2007). This effect can be due to high-quality maternal care *per se*, or because high-quality care signals offspring that they are in a safe environment: the presence of foreign males near a nest poses a risk to pups. In stable conditions, mothers can devote more of their time to intensive brood care, whereas if a male is around, she has to leave the pups more often abruptly to defend the litter against him. Thus, the quality of received maternal care may provide cues to the developing offspring about the social environment outside of the nest and thereby indirectly indicate the environmental risk and social stability of their future environment.

**4 Social cueing.** In addition to individual or social learning and sensory stimulation, social interactions will often provide cues also about the state of the social environment. For example, the composition of social groups can provide indirect cues about local density or sex ratio. As discussed in the previous sec-

tion, however, social cueing is difficult to disentangle from other behavioural mechanisms.

It is unlikely that any of these behavioural mechanisms are restricted to particular taxonomic groups. The fact that even the cognitively more demanding mechanisms, individual learning and social learning, can occur across vertebrates, from fish to mammals, rather suggests that species-specific social ecology and social opportunities determines the occurrence of a given mechanism.

### Understanding Unexpected Effects

Refraining from surveillance of the social interactions that occur during the experimental social experience phase may result in the unsatisfactory situation that we cannot properly interpret the results of our experiment. For example, when the birth spacing of litters in communal nests of mice was wide, old, young and solitarily reared pups performed better in a later-life hierarchy formation task than did middle-aged pups (Branchi et al. 2013a). This result is rather surprising because there was no obvious *a priori* reason to assume that middle-aged pups should be different. Only by observing the interactions in the nest during the experience phase, it became apparent that pups from middle-aged litters received the least maternal care of all litters, which provides an explanation for their poor performance in social challenges later in life. Another unexpected finding was a lower copulation success per song directed to a female in brown-headed cowbird males that had been exposed to adult males as juveniles (White et al. 2002b). During the experience phase in the presence of adults, these males had developed more natural social behaviour in various respects compared to males reared without adults so that rather a higher copulation success should be expected in the males with adult exposure. Detailed observations during the experience phase revealed, however, that adult-exposed birds developed a song with lower potency. This may possibly explain their lower copulation success per song directed to females. Finally, a comparison between biparental and female-only care in Mandarin voles revealed that biparental offspring received more care, which might have been expected; it also revealed that in the presence of males, mothers increased lactation and licking rates as compared to mothers caring alone (Jia et al. 2009), a finding that was less straightforward (alternatively, male care might also lead to load lightening and reduction of female care). Thus, by observing the interactions in the nest, it is possible to formulate two, non-mutually exclusive hypotheses

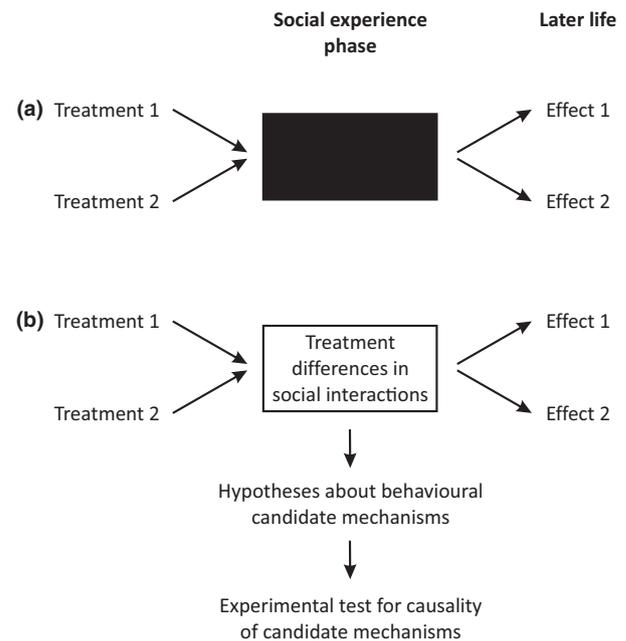
about the behavioural mechanisms responsible for the various long-term effects detected in these mice: they might be caused by (1) the total amount of parental care or by (2) the more intensive maternal care (for more details on all three examples, see Table 1).

As a general note of caution, manipulating social complexity in the laboratory may yield unexpected results, simply because in the laboratory, we are unable to simulate natural social networks of our study species. For example, in a wild cleaner fish population, the interaction frequencies with clients vary between 800/d in a simple habitat and 2000/d in a complex habitat, with important differences between the socio-cognitive skills in the two habitat types (Wismer et al. 2014). Trying to offer a socially deprived vs. enriched treatment to these fish in the laboratory has a high chance to fail due to logistic constraints, so that even in 'enriched' laboratory conditions interaction frequencies would still be magnitudes below the lowest observed frequencies found in the wild.

### Testing for the Causality of Behavioural Mechanisms

I would like to argue in this section that it is important that our research does not end by proposing possible hypotheses about underlying behavioural mechanisms based on observations during the experience phase. In many of the studies reviewed in Table 1, several aspects of the social interactions changed with the social treatments. Moreover, correlation analyses revealed that different aspects of variation in social interactions can affect different later-life traits (e.g. Branchi et al. 2013a). This means that the observation of social interactions during the experience phase of developmental experiments will often give rise to several alternative hypotheses about involved behavioural mechanisms. More importantly, in none of the observed differences of social interactions during the experience phase can we be sure that they are the main cause for later-life traits, rather than other, unmeasured variables. Therefore, a necessary step is to develop targeted experiments testing for the causality of identified candidate mechanism by specifically manipulating the identified property of social interactions (Fig. 1).

I would like to illustrate this point with an example from our work in the cichlid fish *N. pulcher*. We found that young fish of this species reared with parents had a better performance in a suite of social challenges later in their juvenile and adult life compared to fish reared without parents. We had



**Fig. 1:** (a) Opening the black box of social behaviour and interactions during the treatment phases of developmental experiments (b) allows identifying behavioural candidate mechanisms (for example, the frequency or type of a certain social interaction) that might cause long-term effects on behaviour. In a final step, we should manipulate these candidates to prove causality.

observed a higher frequency of among-sibling interactions during the treatment phase in groups reared with parents, and we proposed that this difference in sibling interactions is responsible for the different later-life performance as a consequence of learning appropriate social behaviour by experience. We cannot exclude the alternative hypothesis, however, that the performance of offspring reared with parents was influenced by cues the young obtained from parent about the state of their environment (e.g. chemical or acoustic cues), which may have signalled, for instance, the degree of safety from predation risk (Arnold & Taborsky 2010; Taborsky et al. 2012). Based on these hypotheses, we can perform at least three confirmatory experiments to find out which of these mutually non-exclusive mechanisms are at work. We should manipulate (1) the frequency of among-sibling interactions, (2) the presence or absence of chemical cues produced by parents conveying information about the riskiness of the environment and (3) the presence or absence of predator cues directly perceived by the focal juveniles during early life. If any of these follow-up experiments replicate the long-term effects of our initial experiment (rearing with our without par-

ents), we can be more confident to have identified a causal mechanism.

Two nice examples show how social interactions can be manipulated directly. In Bobwhite quails, parental responsiveness to chicks was manipulated by combining the use of dummies and playback (Harshaw & Lickliter 2007). In rats, a component of maternal care (tactile stimulation of pups) was simulated by the experimenter (Hellstrom et al. 2012). To avoid artefacts, we should think about how to manipulate the candidate interactions between conspecifics rather than relying on the use of dummies or human simulation of interactions. For example, in case of the rats, an elegant way to increase licking and grooming and thereby tactile stimulation in individual offspring of a brood is to add a drop of saltwater to the nape of a pup (M. Schweinfurth, B. Stieger & M. Taborsky, in preparation).

## Conclusions

To conclude, by manipulating the early social environment, we typically alter social complexity through changing the quantity, quality and/or diversity of social interactions. These changes may provide inadvertent cues to the focal animals about the state of their social environment, such as local density, sex ratio, or age and size structure of populations. In addition to inadvertent information, the evidence reviewed here strongly suggests that direct experience from social interactions can significantly contribute to long-term effects on later social performance, for example by improved opportunities to learn how to behave adequately in different social situations in socially more complex early environments. If we are interested in understanding the causes of long-term effects of the early social environment, it seems obvious that social interactions during the experimental experience phase should *always* be recorded. As outlined above, there are at least two arguments for this. Knowledge about how the social interactions differ between rearing treatments (1) permits researchers to formulate hypotheses about candidate mechanisms causing long-term effects on behaviour (Fig. 1) and (2) can help to interpret unexpected outcomes of developmental experiments. Finally, while almost all developmental studies propose hypotheses about the behavioural or neural mechanisms that might have been triggered by manipulations of the social environment, we should proceed and perform confirmatory experiments proving causality of the hypothesized mechanisms.

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## Literature Cited

- Adkins-Regan, E. & Krakauer, A. 2000: Removal of adult males from the rearing environment increases preference for same-sex partners in the zebra finch. *Anim. Behav.* **60**, 47–53.
- Arnold, C. & Taborsky, B. 2010: Social experience in early ontogeny has lasting effects on social skills in cooperatively breeding cichlids. *Anim. Behav.* **79**, 621–630.
- Banerjee, S. B., Arterbery, A. S., Fergus, D. J. & Adkins-Regan, E. 2012: Deprivation of maternal care has long-lasting consequences for the hypothalamic-pituitary-adrenal axis of zebra finches. *Proc. Biol. Sci.* **279**, 759–766.
- Bateson, P. 1994: The dynamics of parent offspring relationships in mammals. *Trends Ecol. Evol.* **9**, 399–403.
- Bentsen, C. L., Hunt, J., Jennions, M. D. & Brooks, R. 2006: Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus*. *Am. Nat.* **167**, E102–E116.
- Benus, R. F. & Henkelmann, C. 1998: Litter composition influences the development of aggression and behavioural strategy in male *Mus domesticus*. *Behaviour* **135**, 1229–1249.
- 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. *Biol. Psychiatry* **60**, 690–696.
- Branchi, I., D'Andrea, I., Gracci, F., Santucci, D. & Alleva, E. 2009: Birth spacing in the mouse communal nest shapes adult emotional and social behavior. *Physiol. Behav.* **96**, 532–539.
- Branchi, I., Curley, J. P., D'Andrea, I., Cirulli, F., Champagne, F. A. & Alleva, E. 2013a: Early interactions with mother and peers independently build adult social skills and shape BDNF and oxytocin receptor brain levels. *Psychoneuroendocrinology* **38**, 522–532.
- Branchi, I., Santarelli, S., D'Andrea, I. & Alleva, E. 2013b: Not all stressors are equal: early social enrichment favors resilience to social but not physical stress in male mice. *Horm. Behav.* **63**, 503–509.
- Burgess, S. C. & Marshall, D. J. 2014: Adaptive parental effects: the importance of estimating environmental predictability and offspring fitness appropriately. *Oikos* **123**, 769–776.

- Champagne, F. A. 2010: Epigenetic influence of social experiences across the lifespan. *Dev. Psychobiol.* **52**, 299–311.
- Champagne, F. A. & Curley, J. P. 2005: How social experiences influence the brain. *Curr. Opin. Neurobiol.* **15**, 704–709.
- Champagne, F. A. & Meaney, M. J. 2007: Trans generational effects of social environment on variations in maternal care and behavioral response to novelty. *Behav. Neurosci.* **121**, 1353–1363.
- Chapman, B. B., Morrell, L. J., Benton, T. G. & Krause, J. 2008a: Early interactions with adults mediate the development of predator defenses in guppies. *Behav. Ecol.* **19**, 87–93.
- Chapman, B. B., Ward, A. J. W. & Krause, J. 2008b: Schooling and learning: early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Anim. Behav.* **76**, 923–929.
- Creel, S., Dantzer, B., Goymann, W. & Rubenstein, D. R. 2013: The ecology of stress: effects of the social environment. *Funct. Ecol.* **27**, 66–80.
- 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. *Front. Behav. Neurosci.* **3**, 25.
- D'Andrea, I., Alleva, E. & Branchi, I. 2007: Communal nesting, an early social enrichment, affects social competences but not learning and memory abilities at adulthood. *Behav. Brain Res.* **183**, 60–66.
- Fischer, B., Taborsky, B. & Kokko, H. 2011: How to balance the offspring quality-quantity tradeoff when environmental cues are unreliable. *Oikos* **120**, 258–270.
- Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A. & Taborsky, B. 2015: Rearing group size determines social competence and brain structure in a cooperatively breeding cichlid. *Am. Nat.* **186**, 123–140.
- Foster, S. A. 2013: Special Issue: Behavioural plasticity and evolution. *Anim. Behav.* **85**, 1003.
- 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.
- Gracceva, G., Venerosi, A., Santucci, D., Calamandrei, G. & Ricceri, L. 2009: Early social enrichment affects responsiveness to different social cues in female mice. *Behav. Brain Res.* **196**, 304–309.
- Groothuis, T. G. G. & Maestripieri, D. 2013: Parental influences on offspring personality traits in oviparous and placental vertebrates. In: *Animal Personalities. Behavior, Physiology, and Evolution* (Carere, C. & Maestripieri, D., eds). Univ. of Chicago Press, Chicago, pp. 317–352.
- Groothuis, T. G. G. & Schwabl, H. 2008: Hormone-mediated maternal effects in birds: mechanisms matter but what do we know of them? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **363**, 1647–1661.
- Groothuis, T. G. & Taborsky, B. 2015: Introducing biological realism into the study of developmental plasticity in behaviour. *Front. Zool.* **12**, S6.
- Harshaw, C. & Lickliter, R. 2007: Interactive and vicarious acquisition of auditory preferences in Northern bobwhite (*Colinus virginianus*) chicks. *J. Comp. Psychol.* **121**, 320–331.
- Hebets, E. A. 2003: Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proc. Natl Acad. Sci. USA* **100**, 13390–13395.
- Hellstrom, I. C., Dhir, S. K., Diorio, J. C. & Meaney, M. J. 2012: Maternal licking regulates hippocampal glucocorticoid receptor transcription through a thyroid hormone-serotonin-NGFI-A signalling cascade. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**, 2495–2510.
- Jia, R., Tai, F., An, S., Zhang, X. & Broders, H. 2009: Effects of neonatal paternal deprivation or early deprivation on anxiety and social behaviors of the adults in mandarin voles. *Behav. Process.* **82**, 271–278.
- Kaiser, S. & Sachser, N. 2005: The effects of prenatal social stress on behaviour: mechanisms and function. *Neurosci. Biobehav. Rev.* **29**, 283–294.
- Kasumovic, M. M. 2013: The multidimensional consequences of the juvenile environment: towards an integrative view of the adult phenotype. *Anim. Behav.* **85**, 1049–1059.
- Kasumovic, M. & Andrade, M. 2009: A change in competitive context reverses sexual selection on male size. *J. Evol. Biol.* **22**, 324–333.
- Kasumovic, M. M. & Brooks, R. C. 2011: It's all who you know: the evolution of socially cued anticipatory plasticity as a mating strategy. *Q. Rev. Biol.* **86**, 181–197.
- Kosten, T. A., Kim, J. J. & Lee, H. J. 2012: Early life manipulations alter learning and memory in rats. *Neurosci. Biobehav. Rev.* **36**, 1985–2006.
- Laviola, G. & Terranova, M. L. 1998: The developmental psychobiology of behavioural plasticity in mice: the role of social experiences in the family unit. *Neurosci. Biobehav. Rev.* **23**, 197–213.
- Liebgold, E. B. 2014: The influence of social environment: behavior of unrelated adults affects future juvenile behaviors. *Ethology* **120**, 388–399.
- 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.
- Liu, D., Diorio, J., Day, J. C., Francis, D. D. & Meaney, M. J. 2000: Maternal care, hippocampal synaptogenesis and cognitive development in rats. *Nat. Neurosci.* **3**, 799–806.

- Love, O. P., McGowan, P. O. & Sheriff, M. J. 2013: Maternal adversity and ecological stressors in natural populations: the role of stress axis programming in individuals, with implications for populations and communities. *Funct. Ecol.* **27**, 81—92.
- Macri, S., Laviola, G., Leussis, M. P. & Andersen, S. L. 2010: Abnormal behavioral and neurotrophic development in the younger sibling receiving less maternal care in a communal nursing paradigm in rats. *Psychoneuroendocrinology* **35**, 392—402.
- Maestripieri, D. 2005a: Effects of early experience on female behavioural and reproductive development in rhesus macaques. *Proc. Biol. Sci.* **272**, 1243—1248.
- Maestripieri, D. 2005b: Early experience affects the intergenerational transmission of infant abuse in rhesus monkeys. *Proc. Natl Acad. Sci. USA* **102**, 9726—9729.
- Magellan, K. & Magurran, A. 2009: The effect of social environment during ontogeny on life history expression in the guppy *Poecilia reticulata*. *J. Fish Biol.* **74**, 2329—2337.
- Margulis, S. W., Nabong, M., Alaks, G., Walsh, A. & Lacy, R. C. 2005: Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*. *Anim. Behav.* **69**, 627—634.
- McCormick, M. I. 2009: Indirect effects of heterospecific interactions on progeny size through maternal stress. *Oikos* **118**, 744—752.
- Meaney, M. J. 2001: Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annu. Rev. Neurosci.* **24**, 1161—1192.
- Meaney, M. J. & Szyf, M. 2005: Maternal care as a model for experience-dependent chromatin plasticity? *Trends Neurosci.* **28**, 456—463.
- Monaghan, P. 2008: Early growth conditions, phenotypic development and environmental change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **363**, 1635—1645.
- Parent, C. I. & Meaney, M. J. 2008: The influence of natural variations in maternal care on play fighting in the rat. *Dev. Psychobiol.* **50**, 767—776.
- Parent, C. I., Del Corp, A., Cameron, N. M. & Meaney, M. J. 2013: Maternal care associates with play dominance rank among adult female rats. *Dev. Psychobiol.* **55**, 745—756.
- Piersma, T. & Drent, J. 2003: Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* **18**, 228—233.
- Rittschof, C. C., Coombs, C. B., Frazier, M., Grozinger, C. M. & Robinson, G. E. 2015: Early-life experience affects honey bee aggression and resilience to immune challenge. *Sci. Rep.* **5**, 15572.
- Ruploh, T., Bischof, H. J. & von Engelhardt, N. 2013: Adolescent social environment shapes sexual and aggressive behaviour of adult male zebra finches (*Taeniopygia guttata*). *Behav. Ecol. Sociobiol.* **67**, 175—184.
- Ruploh, T., Bischof, H. J. & von Engelhardt, N. 2014: Social experience during adolescence influences how male zebra finches (*Taeniopygia guttata*) group with conspecifics. *Behav. Ecol. Sociobiol.* **68**, 537—549.
- Ryan, B. C. & Vandenbergh, J. G. 2002: Intrauterine position effects. *Neurosci. Biobehav. Rev.* **26**, 665—678.
- Sachser, N., Kaiser, S. & Hennessy, M. B. 2013: Behavioural profiles are shaped by social experience: when, how and why. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120344.
- Shea, N., Pen, I. & Uller, T. 2011: Three epigenetic information channels and their different roles in evolution. *J. Evol. Biol.* **24**, 1178—1187.
- Taborsky, B. & Oliveira, R. F. 2012: Social competence: an evolutionary approach. *Trends Ecol. Evol.* **27**, 679—688.
- Taborsky, M. & Taborsky, B. 2015: Evolution of genetic and physiological mechanisms of cooperative behaviour. *Curr. Opin. Behav. Sci.* **6**, 132—138.
- Taborsky, B., Arnold, C., Junker, J. & Tschopp, A. 2012: The early social environment affects social competence in a cooperative breeder. *Anim. Behav.* **83**, 1067—1074.
- Taborsky, B., Tschirren, L., Meunier, C. & Aubin-Horth, N. 2013: Stable reprogramming of brain transcription profiles by the early social environment in a cooperatively breeding fish. *Proc. Biol. Sci.* **280**, 20122605.
- Uller, T. 2008: Developmental plasticity and the evolution of parental effects. *Trends Ecol. Evol.* **23**, 432—438.
- Weaver, I. C. G., Cervoni, N., Champagne, F. A., D'Alessio, A. C., Sharma, S., Seckl, J. R., Dymov, S., Szyf, M. & Meaney, M. J. 2004: Epigenetic programming by maternal behavior. *Nat. Neurosci.* **7**, 847—854.
- West-Eberhard, M. J. 2003: *Developmental Plasticity and Evolution*. Oxford Univ. Press, Oxford.
- White, D. J., King, A. P. & West, M. J. 2002a: Facultative development of courtship and communication in juvenile male cowbirds (*Molothrus ater*). *Behav. Ecol.* **13**, 487—496.
- White, D. J., King, A. P. & West, M. J. 2002b: Plasticity in adult development: experience with young males enhances mating competence in adult male cowbirds, *Molothrus ater*. *Behaviour* **139**, 713—728.
- 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. *Anim. Behav.* **79**, 385—390.
- 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.