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### Living in a changing world

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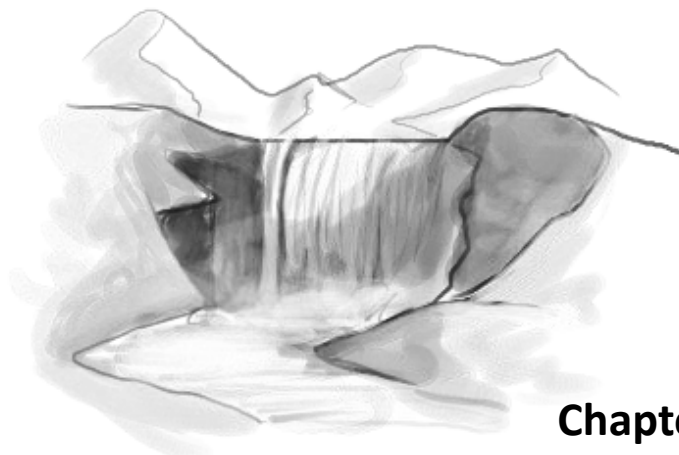
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**Chapter 6:**  
**Why and how the early-life environment**  
**affects development of coping behaviours: a**  
**review**

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*In prep.*

## **Abstract**

Understanding the ways in which individuals cope with threats, respond to challenging situations and mediate the harmful effects of their surroundings is important for predicting both animal and human ability to function in a rapidly changing world. Although the study of coping (the behaviours displayed in response to environmental challenges) knows a long and rich research history in biology, recent literature has repeatedly pointed out that to date the processes through which coping behaviours develop in individuals are still largely unknown. Perhaps one of the most essential drivers of coping behaviour of adults is the environment as experienced during the formative period. In this review, we make a move towards integrating ultimate and proximate lines of research. We consider why from an evolutionary perspective the development of coping has become tightly linked to the early-life environment. Furthermore, we ask how that environment affects expression of coping behaviours, by asking 1) which (epi)genetic and non-genetic developmental processes are important in creating coping behaviours; 2) which types of early-life influences affect the development of coping behaviours during different stages of life, and 3) how parental coping styles can be transmitted to their offspring. Finally, we discuss the extent to which developmental processes create stability or leave animals stuck with behaviours that are based in past conditions, as intergenerational transmission may also have maladaptive aspects in the light of environmental change.

## 6.1. Introduction

Coping is a broad concept that has been defined in many different ways across many fields. In biology, coping is commonly considered as the behavioural and physiological efforts to master a challenging situation (Koolhaas et al 1999). In psychology, coping is often regarded as “the thoughts and behaviours used to manage the internal and external demands of situations that are appraised as stressful” (Folkman et al 1986) or similar wording (Compas et al 2004), while others define it as “action regulation under stress” (Skinner and Zimmer-Gembeck 2007a). As such, it is closely linked to concepts such as (animal) personality, behavioural syndromes and emotion regulation. While coping and personality have been linked many times (McCrae and Costa 1986; Jang et al 2007; Carver and Connor-Smith 2010b; Kaiseler et al 2012), and are sometimes used interchangeably (Melotti et al 2011), they cannot be considered identical. Although coping and personality play both independent and interactive roles in influencing physical and mental health, the influence of personality on coping, and of both on fitness measures, is only partially understood (Olff et al 1993; Carver and Connor-Smith 2010a).

Despite the long research history in coping and the great interest in the topic across both animal biology and psychology, only very little is known about the way coping behaviours develop in individuals (Belsky and Pluess 2009a; Stamps and Groothuis 2010; Rao et al 2010; Gracceva et al 2011; Groothuis and Trillmich 2011b). In animal biology, much attention is currently focussed on finding evidence of individual differences in coping behaviours across different species (Bell and Stamps 2004; Dall et al 2012; Ogden 2012), understanding the active-reactive axis on which such coping behaviours seem to fall (Sloan Wilson et al 1994; Koski 2011; Pascual and Senar 2014), explaining the evolutionary mechanisms underlying individual differences (Dingemanse et al 2002; Adriaenssens and Johnsson 2011), and integrating its implications for ecological and behavioural studies. The field of psychology is in a different place, and emphasises largely on coping in relation to stress and various forms of psychological distress (Arran et al 2014), such as the way children deal with actual stressors in real-life contexts (Skinner et al 2003). Even though a great deal of mainstream developmental research is devoted to understanding whether and how experiences in ontogeny shape psychological and behavioural development later in life, little theoretical attention has been paid to why such cross-time influences should characterize human (Belsky 2007; Ellis and Boyce 2008; Haun et al 2013) or animal (Skinner and Zimmer-Gembeck 2007a; Groothuis and Trillmich 2011b; Trillmich and Hudson 2011b) development, or how natural selection structures the early-life effects on that development (Ellis and Boyce 2008). Selecting developmental influences (such as parental depression (Langrock et al 2002)) and correlating them with one or more behavioural traits is very important for discovering variables relevant to shaping behavioural traits, yet it does not provide clarity on the proximate and ultimate aspects of the development of coping

behaviours (Groothuis and Trillmich 2011b), and no overarching developmental framework for the study of coping currently exists (Skinner and Zimmer-Gembeck 2007a).

Within the development of coping behaviours, there is an important unexplored niche in the ways through which environmental experiences during early-life development shape the coping behaviours used later in life. Yet this early-life period is extremely relevant, as costs, limitations and opportunities experienced during ontogeny affect the development of coping behaviours, and as such directly affect the range of possible behaviours individuals have available later in life (Rödel and Monclús 2011). Individuals may begin on the same developmental trajectory, yet display very different patterns of (mal)-adaptation. The pathway to either psychopathology or resilience is influenced by a complex matrix (Cicchetti 2010), in which environmental factors such as past and current experiences, the social context, timing of the adverse experiences are key factors. Such influences may begin prenatally, and postnatally be amplified as individuals come to occupy different niches within their surroundings, interact with conspecifics and cope with environmental challenges (Hudson et al 2011; Trillmich and Hudson 2011b).

In this paper, we offer an environmental perspective on the development of coping and consider the process from an evolutionary angle. Without going too deeply into neurobiological details, we consider ultimate and proximate cause of early-life influences on adult coping strategies. Ultimately, we do this by reviewing requirements for successful coping and the evolutionary concepts important in development of coping behaviours. Proximally, by 1) categorising which (epi)genetic and non-genetic developmental processes drive the development of coping behaviours; 2) considering empirical studies that report early-life influences on the development of coping behaviours during different stages of life and from this distilling important environmental factors, and 3) considering transmission of such coping behaviours, once acquired, to the next generation. This approach allows us to understand more closely why some environmental factors affect development of coping differently than others and in what direction, and apply that understanding to mental health concerns and challenges adapting to new environments. Covering the concept of coping from evolutionary, ethological, psychological and neurological perspectives, along with the interconnections and complex relationships between all of its aspects, falls far outside the scope of this review. For the purpose of this review, to avoid confusion in terminology, we discuss *coping behaviours*, defined here as the behaviours that individuals give aimed at responding to environmental challenges. This includes behaviours commonly used in animal biology such as approach, avoidance, aggression, sociality, boldness and exploration. Where they are clearly relevant to coping behaviours, we also discuss human and animal personality traits such as anxiety, stress response, or social behaviour.

## 6.2. Why the early-life environment affects coping

In order to survive and meet their basic needs, all animals constantly interact with their environment. They search to acquire food and other resources, watch for predators and other danger, and secure a safe place to rest. They interact with animals of their kind, attempt to find a suitable mate and take care of their offspring. From an evolutionary perspective, coping behaviour is an animal's first line of defence against harsh circumstances. When coping strategies fail, the individual is likely suffer negative consequences (Koolhaas et al 1999). Such consequences can express on a physical level, as animals may be predated upon or experience hunger if they do not respond adequately to environmental challenges, but may also express on an emotional level, as is the case for example in social defeat (Benus et al 1991). Failure to cope can, directly or indirectly, result in an animal's death. As such, they are a target for natural selection processes, and there is ample evidence for heritability in coping behaviours, although values tend to differ per species, behaviour, and type of measurement (Benus et al 1991; Dingemans et al 2002; Jang et al 2006; Rice 2008).

To ensure optimal survival and reproduction, natural selection would be expected to fine-tune development of coping behaviours to environmental circumstances that are likely to affect the animal during its life. Empirical work shows that populations from different environments do indeed display different coping behaviour. For example, three-spine sticklebacks from predator-experienced populations showed relatively more aggression and stress responsiveness than sticklebacks from predator-naive populations, and correlations between boldness, aggressiveness and exploratory behaviour were found in populations where predators were present (Dingemans et al 2007; Bell and Sih 2007; Bell et al 2011). Selection is expected to favour development of those coping behaviours that increase the individual's ability to accurately respond to threats and to most effectively utilise opportunities to its benefit. In this section, we detail some requirements for successful coping and why early-life influences are important in meeting these requirements.

### 6.2.1 Sensitivity to early-life environment

When young animals are born, they know nothing of the surroundings they have to survive in, the challenges ahead, or exactly what strategies are effective in dealing with predators, within the social hierarchy, and in obtaining resources. In order to survive, they need to develop the skills and behaviours necessary to interact successfully with their environment. The more accurately coping behaviours are tuned to the environment, the better the animal's chances of survival and eventual reproductive success. Sensitivity to conditions experienced during early-life increases animal's chances of developing behaviours that are functional within their surroundings. If young individuals experience an unsafe environment in which their life and health are in constant danger, it is beneficial to them to develop

keener senses, build cognitive database on hiding places and learn to respond to unexpected stimuli by freezing in place or bolting for cover. If on the other hand they experience a safe environment, there is a greater benefit to engaging a new situation and exploring unexpected stimuli as there is little risk and the opportunity of finding additional resources. In line with this reasoning, a large body of evidence indicates that the environment young animals experience is essential in determining how they develop their coping behaviours (see section 6.3). For example, young who grow up in a large family context develop a greater awareness of social subtleties than young who receive only a little social stimulation (Branchi 2009; Ahern and Young 2009).

From an evolutionary perspective, there is a distinct benefit to maintaining developmental processes that facilitate fast and targeted learning in the very first stages of life and that fine-tune coping behaviours to existing environmental conditions. Such processes allow animals a degree of flexibility and adaptability across generations, and increase the chances that young are capable of responding quickly and appropriately to surroundings that they do not yet have the personal experience with. As a consequence of processes such as habituation and early perceptual learning (Beach and Jaynes 1954), various factors in the early-life (see section 6.3.4) may affect the developmental trajectory that individuals follow (Rödel and Monclús 2011), the kind of experiences they have during their life, and the way they interact with conspecifics. As such early-life have a major influence on the behaviours adults use to cope with their environment, and in which situations they display them. Conversely, sensitivity to early-life circumstances may create a vulnerability to behavioural mismatch with the environment later in life (Raubenheimer et al 2012; Jensen et al 2014) or when the environment changes (Roberts et al 2011).

## 6

Recently, now that researchers start to work increasingly from a post-genomics outlook, the environment is more and more considered as crucial as the DNA sequence for constructing the phenotype, and as a source of information in predicting the phenotype (LaFreniere and MacDonald 2013).

### 6.2.2 Requirements for successful coping

In this section, we have a closer look at the ultimate reasons for sensitivity of coping behaviours to the early-life environment. For all animals, successful adaptation to environmental conditions depends on *perceiving* a need for a response, *estimating* an effective response, *being able* to give that response, and *paying the cost* for that response. For example, in order to cope with a larger animal encroaching into its habitat, a rabbit has to have a sensory awareness of the other animal, followed by the perception that the other is either harmless or dangerous. If the latter, the rabbit has to estimate whether to hide or run, and whether it is physically capable of running fast enough to be successful. If it does run, it can lose foraging time, valuable resources or encounter other dangers, which it may

not be able to afford (Papworth et al 2013). There is strong selection on individuals' ability to accurately perceive an environmental threat, challenge or opportunity, estimate which coping behaviour to give, and then respond with minimal cost, as there are immediate and possibly life threatening consequences to responding with the wrong behaviour. To a large extent, the early-life conditions are what determine an individual's ability to fulfil these requirements effectively. Below we detail these four requirements for successful coping, and how they relate to the early-life environment.

### 6.2.2.1 Cognition

Perceiving a threat is a first and necessary step to coping (Edenbrow and Croft- 2013), whether that perception happens on a conscious or unconscious level (Lovibond and Shanks 2002). Animals cannot respond to dangerous situations that their sensory systems cannot perceive (Shettleworth 2001; Guesdon et al 2011). Herein also lays a vulnerability, one that has been mostly explored within the domain of psychology (Brewer et al 2007; Arran et al 2014). The perception of a threat can be inaccurate, thereby preventing successful coping from the start. Individuals may fail in sensory perception of a threat, or fail to perceive a situation accurately enough to consider it a threat. For example, iguanas who were confronted with an approaching human, moved earlier, ran earlier and ran farther when the human's face was exposed vs. covered by hair, as a covered face gave the conflicting stimulus of both approaching and retreating (Burger and Gochfeld 1993). Alternatively, individuals may perceive a threat where there is none, for example in animals that are overly-easily startled or human fear for spiders, water, and other irrational phobias (Adriaens and Block 2011).

In order to perceive threats more accurately, both animals and humans attempt to increase vigilance. Perceiving the environment with accuracy for an extended period of time in order to detect potential dangers is costly, as it takes away from other activities such as foraging, which some species of animals address by increasing group size and sharing vigilance (Eilam et al 2011). As a result, group living animals have evolved processes that acquire and evaluate information (Liddell et al 2004), and a sensitivity to alarm displays from conspecifics (Liddell et al 2004; Brown et al 2006; Rieucau et al 2014) as well as cues directly from predators (Rieucau et al 2014).

As there is little room for trial-and-error, young animals learn risk appraisal early on, and as a result the situations they perceive as a threat or a danger later in life is closely linked to early-life conditions. An individual responding aggressively in certain situations may be doing so because their early-life environment has induced a heightened threat perception, or may respond impulsively because their experiences did not prepare them for the possibility of a predator (Bell et al 2011; El Balaa and Blouin-Demers 2011). Although in



animal biology, it is widely recognised that threat perception is an important aspect of animal functioning (Burger and Gochfeld 1993; Kirschvink 2000; Rieucou et al 2014; Chamaillé-Jammes et al 2014), threat perception and differences therein based on early-life environment are rarely linked to the development of coping behaviours (Brown et al 2013). In part, this is because risk perception (degree of “fear”) is a difficult to study in animals (Stankowich and Blumstein 2005) and especially difficult to separate from the subsequent response.

### 6.2.2.2 Response estimation

Estimating an effective response to a situation can be defined simply as carrying out any response that successfully mediates the situation to where there is no longer a threat. When an individual does not correctly estimate which response should be given, it creates a mismatch between behaviour and environment that can be fatal to the animal (DiRienzo et al 2012), as can be observed for example when captive-bred fish are challenged to respond to predator cues and respond less appropriately than wild bred fish (El Balaa and Blouin-Demers 2011). Such a mismatch also occurs when individuals respond too readily to possible threats. Responding only to individuals of a predator species which display sufficiently threatening behaviour allows prey species to minimise energy expenditure and other costs of predator avoidance, which is especially relevant if the predator is common but attacks are infrequent (Papworth et al 2013).

It must be noted that the coping responses that animals display are often non-conscious and part of a stimulus-response bond (Liddell et al 2004), a pathway that has become engrained through a myriad of developmental processes (see section 6.3.3). Yet there is indication that animals, consciously or otherwise, choose from multiple available strategies when environmental conditions incite them to respond to a threat. Which strategy is estimated as the most effective, is dependent upon current environmental conditions as well as past experience and the animal’s personal success rate with the available coping strategies. The threat-sensitive predator avoidance model (Bishop and Brown 1992; Brown et al 2006; Rieucou et al 2014; Chamaillé-Jammes et al 2014) predicts that animals should take into account perceived predation risk to balance the intensity of their antipredator response, which may be a graded response pattern, nongraded, or “hypersensitive”. Recent work on cichlids showed that when threatened, individuals exhibited reduced time moving and foraging than shoals, and small shoals exhibited a higher response threshold than large shoals (Brown et al 2006). Similarly, wild caught herrings provided the strongest avoidance reactions when exposed to versatile predator sensory cues (Rieucou et al 2014). These findings and others (Bishop and Brown 1992) indicate that response patterns are flexible and situation dependant, and subject to natural selection processes.

As much as threat perception, threat evaluation is dependent at least to a degree on experiences during the early-life. A factor that plays a role in estimating behavioural responses is sufficient familiarity with the situation and habituation, which is built through either personal experience with similar situations earlier in life (Snell-Rood et al 2013), or learning from others who previously experienced the situation (Brown et al 2006; Rieucou et al 2014). Good other examples of responses influenced by early-life conditions are pets no longer perceiving humans as threats and vice versa or stress response to perfectly normal situations because of trauma earlier in life, but also sensitivity to alcohol because a parent was alcoholic. The ability to estimate which response to take under different circumstances is especially relevant in coping with novelty, when little previous experience is available (Tang et al 2011).

### 6.2.2.3. Ability

Even when a challenge has been perceived and an appropriate response has been estimated, successful coping is not guaranteed. Animals may not be able to give the response that is most effective, due to physical or emotional constraints (Long 1990; Leichty et al 2012).

Beyond limitations on a species level, emotional constraints that prevent animals from giving a healthy response often originate from negative experiences earlier in their lives. Stressors or deprivation early in life may have made it impossible to give a healthy response. For example, the nest environment in young rats was shown to affect ontogeny of personality types, with heavier individuals being more bold and more explorative, and individuals from both small and large litters being more anxious than individuals from medium sized litters (Rödel and Meyer 2011). In addition, development of behavioural processes may have canalised (Hermanussen et al 2001) in a direction that excludes the desired behaviour, but cannot be reversed. In animal ecology, correlated behavioural suits (analogous to human personality (Dingemanse and Wolf 2010), have been linked to constraints in behavioural plasticity, the extent to which an individual can change its behaviour or development in response to environmental cues (Dochtermann and Dingemanse 2013), see section 6.2.3).

### 6.2.2.4. Cost of response

Finally, if an animal responds with a particular coping behaviour, it must be able to incur the costs of that behaviour or the coping response will lead to a loss of fitness rather than a gain, either immediately or over a longer time span. Such costs can come in many forms. An animal that responds to the appearance of a competitor at the feeding ground with flight, freezing or hiding, loses the opportunity to forage and obtain resources. An animal

that responds with aggression, on the other hand, may incur cost to its physical health sustained in fighting displays. If the aggression is part of a behavioural construct, where the same coping behaviour is displayed across contexts (Bell and Stamps 2004), the individual may incur costs when that same aggression gets it eaten by a predator.

An animal's ability to respond with an adaptive coping behaviour, as well as the cost of that coping on health in the moment or across other contexts in life, are both linked to early-life experiences (Fish et al 2004a; Rödel and Monclús 2011), as physically stronger or behaviourally more flexible individuals may be more resilient to costs of coping behaviours, both of which traits are determined throughout the individual's life history.

### 6.2.3 Development of individual differences

Young mammals are born with a lot of behavioural plasticity, allowing juveniles to have a lot of flexibility in the coping behaviours they can display in response to different situations (Dufty Jr et al 2002; Belsky and Pluess 2009a; Mery and Burns 2010). Plasticity has been considered especially important in short term adjustment to novel environments (Gross et al 2010). Yet instead of maintaining plasticity, environmental influences during development induce canalisation of coping behaviours into patterns that are often stable and consistent across contexts. This has long been obvious in psychology (Derryberry et al 2003), and has more recently also been widely recognised in animal behaviour, where such stability is commonly referred to as a behavioural syndrome or animal personality (Koolhaas et al 1999; Dingemanse et al 2007; Bell et al 2009; Dall et al 2012). As a result, coping behaviours generally do not fluctuate around the most adaptive behaviour that individuals can give depending on their environment. Instead, individuals come to differ in the coping behaviours they use in throughout life (Wilson and Krause 2012). For example, animals who have a tendency to be generally aggressive may show more aggression towards intruders, but often also show more aggression across other contexts, such as interaction with mates, towards offspring or even towards predators (Bell and Stamps 2004; Bell and Sih 2007). These differences are often consistent within individuals (McGue et al 1993; Derryberry et al 2003; Bell and Stamps 2004; Caspi et al 2005; Dall et al 2012; Dochtermann and Dingemanse 2013), and represent heritable, fundamentally different but equally valuable alternate strategies to cope with environmental demands (Benus et al 1991). In animals this has been studied mostly in terms of the shy-bold axis (Sloan Wilson et al 1994; Toms et al 2010), although recent work shows that other dimensions may also be of importance (Koolhaas et al 2007).

Development of individual differences in coping behaviours is important from an evolutionary point of view, because it signifies the capacity of juveniles to match their stress-response systems to anticipated developmental environments (Boyce and Ellis 2005b), but is also important in understanding and predicting the different ways in which

individuals deal with stress and handle change. Much attention has been focussed on the evolutionary processes that could allow individual differences in personality and coping skills to emerge and remain stable throughout natural selection (Wolf et al 2007b; Wolf et al 2008; Dingemanse et al 2012). It has been especially puzzling why animals behave consistently when behavioural plasticity is so advantageous for responding to environmental conditions (Bell et al 2009), and when canalisation can be disadvantageous.

Individual differences in coping behaviours are considered at least partially a result of varying conditions experienced during the early-life environment and a subsequent interplay between plasticity, developmental stability and canalisation of coping behaviours across contexts (Debat and David 2001). Such a process can explain behaviours that appear strikingly non-adaptive in an isolated context, such as sexual cannibalism or inappropriately high activity when predators are present (Sih et al 2004). The care that juveniles are exposed to early in life (Fleming et al. 2002), and the experiences they have (Rosenzweig and Bennett 1996; Mery and Burns 2010; Frankenhuis and Panchanathan 2011) influence the extent to which individuals canalise coping behaviours in a particular direction. Some individuals canalise their behaviours very strongly, whereas other individuals remain more flexible and will choose behaviour plastically depending on the situation (Terracciano et al 2010). In animals, individual differences in aggression have been shown to be heritable alternative strategies to coping with environmental demands (Benus et al 1991), and field studies have shown heritability of exploratory behaviour in the wild (Dingemanse et al 2002). Individual differences in coping behaviours relate to individual differences in susceptibility to stress and negative influences, but importantly, also to overall biological sensitivity to environmental cues (Boyce and Ellis 2005a; Ellis et al 2011), which can explain why individual differences in behaviour exist even for genetically identical twins growing up within a shared family environment (Asbury et al 2003). In addition, it has been suggested that there are also individual differences in underlying systems that are thought to facilitate individual's capacity to plan effective coping behaviour, and that allow for the coping process to begin before a stressful event (Derryberry et al 2003).

As environmental conditions such as habitat, food availability and predation pressure are different across time and distance, the available resources and the information young animals perceive about their surroundings are important cues for behavioural development. Studies illustrating early-life effects on plasticity and canalisation point to the importance of considering the overall developmental trajectory of an animal when assessing the adaptive value of variation in coping behaviours and other phenotypic traits (Dufty Jr et al 2002), a broader approach than has previously been done by studying the cost of maintaining phenotypic plasticity, which has been reviewed extensively elsewhere (DeWitt et al 1998; A. Relyea 2002; Auld et al 2010).

### 6.2.4 Evolutionary advantages of non-genomic transmission

Recent work has begun to describe evidence that individual differences in coping behaviours, as developed as a product of the parents genetic makeup and their life history, can be passed on to the next generation without an underlying genetic basis for the behaviour, a phenomenon often referred to as non-genomic transmission (Champagne and Meaney 2001) or trans- or intergenerational effects (Thornberry et al 2009; Curley et al 2009; Matthews and Phillips 2010). Although non-genomic transmission of behaviour has to date been extensively studied in the field of psychology, for example in child abuse (Maestriperi 2005; Kwako et al 2010), aggression (Truscott 1992; Neugebauer 2000) and fear of failure (Elliot and Thrash 2004), more recently biologists as well have begun to study intergenerational effects on animal coping behaviour, such as responsiveness to stress in macaques (Kinnally et al 2013) and maternal care in rats (Champagne and Meaney 2007).

Much of evolutionary theory is built on the understanding that behaviours need to have a genetic basis in order for selection to act on them and transmit them to the next generation. However, recent studies on intergenerational effects across many species have challenged this understanding by showing that heritability of behavioural traits is possible without changes in the DNA sequence (Branchi 2009). As much as genetic mechanisms are essential building blocks for the development of behaviour and personality, the way they come to expression and the timing at which they come to expression is often closely linked to the environment that an individual experiences throughout development (Bouchard and McGue 2003; Enoch et al 2010; Nederhof et al 2010). In humans, this is evidenced in the development of obesity, which had long been thought to develop due to interactions between genotype and lifestyle, seems to be caused less by genetics and more by maternal, familiar and environmental influences during development that allow phenotypic effects to transmit across generations (Muhlhausler et al 2008; Wells 2011). Epigenetic mechanisms are considered important contributors to the processes by which early-life experience affects coping behaviours (Fish et al 2004a; Holmes et al 2005; McClelland et al 2011), for example through fine-tuning of the expression levels of key neuronal genes, governing learning and memory throughout life (McClelland et al 2011). It has been proposed that specific genes function much like “plasticity factors” that govern susceptibility to environmental influences (Belsky and Pluess 2009b). As such, even though coping strategies may be transferred from one generation to the next without a genetic basis, the mechanisms that allow this to happen are encoded in the genetic makeup of the species (Rosenzweig and Bennett 1996; Grether 2005; Leichty et al 2012), and the underlying physiology and the (epi)genetic architecture underlying phenotypic responses to the environment (Herman et al 2014) are subject to natural selection.

In order for non-genetic transmission mechanisms to evolve, they must have (had) some benefit to either the parent, or the offspring, or both. Evolutionary theory suggests several such benefits, most importantly environmental prediction (Burgess and Marshall 2011): in reasonably stable and predictable environments, offspring gain a distinct advantage if their parents can pass on their own experience with the ecological conditions, and prime them for the situations they are likely to face in life. It allows juveniles to quickly obtain complicated responses and display behavioural strategies that proved successful to their parents, without having to take risks and gain experience with the environment themselves. However, this has been shown to not always favour the offspring (Wells 2003; J. Marshall and Uller 2007), especially in situations where the environment experienced as a juvenile does not match the environment experienced at adulthood (Wells 2007a), or when environmental cues are not accurately perceived by parent or offspring (Paglianti et al 2010; Bocedi et al 2012). Another benefit to both fathers and offspring concerns parent-child resemblance and parental investment: this theory is based on the understanding that males, unlike females, cannot be certain about paternity, and should provide less paternal investment to children who are unlikely to be their offspring (Bressan 2002; Apicella and Marlowe 2004; Anderson 2006; Heijkoop et al 2009). This relationship between paternal investment and father-child resemblance in physical traits has indeed been found in many studies (Platak et al 2002; Heijkoop et al 2009; Alvergne et al 2009), although it has not been shown if this relationship is unidirectional. It is expected for males to have developed ways to estimate relatedness through cues of physical and behavioural resemblance, and for offspring to have developed methods to increase resemblance to fathers also in cases where the father is not genetically related. For example, it was recently discovered through cross fostering experiments in zebra finches that exploratory behaviour of foster parents, but not that of the genetic parents, was predictive of the exploratory behaviour of offspring (Schuett et al 2013).

### **6.3. How the early-life environment affects coping**

Even though the environment is considered to have an important role on developmental processes and the evolutionary factors underlying coping are becoming clear, the ontological processes through which coping behaviours emerge and remain stable within individuals have been studied to a much lesser degree (Stamps and Groothuis 2010; Groothuis and Trillmich 2011b), and the mechanisms leading to coping behaviours later in life are largely unexplored (Haun et al 2013). Understanding the interplay between environmental influences and developmental processes assists in predicting which environmental influences can be harmful under which conditions, which stages are especially critical for receiving important environmental input, which types of maladaptive coping behaviours may be reversed, and how interventions can approach such reversibility.

In this section, we review the literature to shed light on the way coping behaviours develop, by categorising the developmental processes impacted by environmental factors and providing an overview of the early-life influences that have been shown to affect later-life expression of coping behaviours. Specifically, we address the following questions: 1) Which developmental processes are important in creating animal coping behaviours? 2) Which early-life influences affect the development of animal coping behaviours? 3) How do coping behaviours of the parents transmit to their offspring through early-life influences? It is expected that there will be a lot of variation both within (Belsky and Pluess 2009b) and between species in the extent to which environmental influences impact the different developmental systems. Given the structured and inherently canalising nature of developmental processes (Ellis and Boyce 2008), cross-species patterns are expected in the types of environmental influences that matter at different stages of development.

### 6.3.1 Methods

**Search strategy:** The ISI database and Google Scholar were searched late August 2014. One search was conducted to identify articles that addressed processes responsible for the development of coping (question 1), and the early-life influences on the development of coping behaviours such as boldness, shyness, avoidance, and predator-responses (question 2). A second search was done to identify studies on intergenerational transmission of coping behaviours (question 3). Manual searching was done on reference lists of included articles and relevant papers from this source were included as well.

**Identification of eligible studies:** Studies in English were included when they presented studies that related any early-life influences to coping styles, correlations between behaviours and behavioural syndromes or personality. Results were excluded when they did not contain reference to behaviours aimed at mediating environmental challenges and included when they concerned behaviours that affect dealing with environmental challenge, which we feel includes social behaviour (Haller et al 2014). Eligible studies on developmental processes (question 1) were included when they showed either empirical work demonstrating effects of such processes, or evolutionary theory indicating why such processes are expected to be important in development. Where multiple behaviours were reported as a result of a single environmental influence, such behaviours were grouped and included together rather than separately in Table 6-1. Studies were excluded if they did not report previously unreported empirical or theoretical work, or when they concerned behaviours not linked to coping with environmental challenges.

**Evaluation of eligible studies:** Data were entered into a spreadsheet and checked for discrepancies by an independent external researcher. Discrepancies were resolved by consensus. Important findings and implications from relevant studies were distilled and represented in sections 6.3.2 – 6.3.5.

**Data presentation and synthesis:** In studies included for questions 1 and 2, information was distilled on the kind of behaviours involved, and the type of environmental influence related to these behaviours. Empirical studies for questions 2 and 3 were displayed in a table, relevant information from reviews was summarised in the text. Where available, the developmental stage(s) during which environmental influences occurred were noted as well. In all cases, where provided, we recorded the following factors: study species, age of the measured individuals, rearing and experimental environment, as these factors have been shown to be of relevance in the expression of animal behaviour (see chapter 4). Such an overview allows us to categorise areas of interest in the literature, and gain insight in the breadth of relevant environmental factors.

### 6.3.2 Results

The literature search generated 761 unique results, 703 of which were excluded as not meeting the criteria. 498 titles did not concern coping behaviours as defined in our methodology, a further 93 did not concern early-life influences, and an additional 112 did not concern animals but humans or plants. From the literature, 89 titles/abstracts were included. An additional 31 were included after examining the references of included papers. Of all included papers, 62 were empirical studies and 27 were reviews. A total of 9 studies addressed question 1, 64 studies addressed question 2, and 16 studies addressed question 3. Several papers discussed both the effects of early-life conditions on individuals, and effects on their offspring. Rodents were the most heavily represented study species (27 studies, 19 of which were on rats), followed by various species of fish (13), birds (12), bigger mammals (9, including cows, horses, dogs) and monkeys (6). By far the majority of studies were conducted under laboratory conditions, with exception of a few who were raised in the wild (Kelley et al 2005; Moretz et al 2007a; Wisenden et al 2011; Roedel and Monclus 2011; Sweeney et al 2013).

Analysis of all selected studies indicated several specific influences of interest, some of which have large areas of overlap. Parental care was the most prevalent early-life influence studied (18%), consisting of several different influences. Negative parental care was studied through maternal separation (6 studies) and impaired maternal care (4 studies). Other ways to ascertain the influence of parental care were through maternal licking and grooming behaviour, early social attachment to mothers, mother-child experiences, exposure to a substitute mother and parental personality traits. Parental care was especially studied in the context of intergenerational effects (63% of studies included for question 3), and much less so in the context of early-life effects alone (19% of studies included for question 2). Social influences were the main focus in 13 studies, through social experience / communal rearing, litter size and sex ratio, sibling competition and other relationships, and various expressions of social complexity and stability. Habitat conditions, measured mainly through



wild vs. lab environments and the quality of housing conditions, were the focus in 10 studies. Less studied early-life influences were nutrition (7 studies), predation (5), abiotic conditions such as light (5), health (4) and sensory input (2). These influences were studied across different stages of early-life: in utero (10% of the studies that specified stage), first week post birth (27%), nursing to weaning (25%), nesting (16%), and fledging (2%). A number of studies took a broader approach of several intervals or a longer period up to six months post birth (10%).

Coping was measured across many different behaviours, most notably exploration (12% of all coping behaviours reported), aggression (10%), boldness (10%) and social behaviour (9%). Other commonly studied coping behaviours (less than 5 studies) included anxiety, stress responsivity, mothering behaviours, foraging, activity, social dominance, and response to novelty. Across these behaviours, there is some inconsistency in terminology, and some overlap between concepts. For example, stress responsiveness is an important coping behaviour, but was represented diversely by gestational stress (Champagne and Meaney 2006), maternal separation (Biagini et al 1998), social isolation (Tuchscherer et al 2006), foraging demands (Kinnally et al 2013), or not clearly defined at all in abstract or title. Certain behaviours were often found studied together. Overall, maternal behaviour, social deprivation and isolation are often considered in intergenerational studies; social stress, anxiety and aggression are mostly studied in rodents and related to human research; and exploration, boldness, and foraging are generally considered by biologists to understand animal personality.

### 6.3.3. Processes underlying development of coping behaviours

We discuss in this section a few key biological processes that affect development of coping behaviours during the early years of life. In answer to question 1, we found the following developmental processes mentioned within included reviews: maternal effects (Broadhurst 1961; Fish et al 2004a; Badyaev and Uller 2009; Wisenden et al 2011; Reddon 2012), imprinting (Hoffman and Ratner 1973; Remy 2010), habituation (Beach and Jaynes 1954), conditioning (Hoffman and Ratner 1973; Groothuis and Mulekom 1991), perceptual learning (Beach and Jaynes 1954) and social learning (Fairbanks 1989; Maestripieri 2005).

We briefly discuss here six of the more important processes: maternal effects, filial imprinting, early perceptual learning, habituation, conditioning, and social learning. While genetics and epigenetics were mentioned often as proximate causes to the development of coping and as processes through which the environment affects behaviour, they represent a mechanistic, building-block level explanation rather than address the functional processes through which coping behaviours develop, and as such were not included as processes. Furthermore, the consensus among recent studies appears to be that environmental factors affect the expression of genetic material in a multitude of ways, and as such

epigenetics likely underlie all developmental processes. Rather than exhaustively and mechanistically covering each process, an effort better left to experts within these fields, we illustrate the relevance of the developmental processes found in the literature in creating coping behaviours and illustrate key differences between them in onset and development.

### 6.3.3.1 Maternal (and paternal) effects

Maternal effects, defined as the direct effect of a mother's phenotype on that of her offspring (Bernardo 1996b; Reddon 2012), have been researched in detail both in animals and humans over the past few decades. Developmentally, they relate to the need for developing systems to receive the appropriate (amount of) stimuli. Environmental factors that have been shown to induce maternal effects and in this way influence offspring coping behaviours, include maternal stress (Thornberry et al 2009), and other versions of maternal care (see section 6.3.4.2). It is becoming increasingly evident that maternal exposure to adversity during pregnancy can lead to life-long effects in offspring (Matthews and Phillips 2010). For example, offspring of mothers who smoked during pregnancy, were more likely to exhibit behavioural disorders including externalising and internalizing problems, and conduct disorders (Abbott and Winzer-Serhan 2012). Effects of maternal stress during pregnancy on behavioural outcomes in the first generation offspring are thought to be highly dependent on species, sex and age (Sullivan et al 2011b), as well as on the time in pregnancy when stress is experienced (Matthews and Phillips 2010). Maternal effects have also been found in across many species beyond effects of stress during the gestation period (Bernardo 1996b). The topic knows a rich literature of its own (Badyaev and Uller 2009) that falls outside our scope to review in its entirety.

More recently, paternal effects have received more interest as well, although compared to maternal effects, still much less is known regarding the role of paternal factors (Rodgers et al 2013). The most significant difference between maternal and paternal effects is the gestation period, during which the maternal phenotype is in intimate physical contact with that of the offspring, which allow for nourishment and hormones to pass from mother to child. Early-life influences that affect offspring coping behaviours through paternal effects, though few have been studied to date (Alvergne et al 2009; Rodgers et al 2013), include non-genomic transmission of personality traits in zebra finches, as demonstrated by cross-fostering experiments where juveniles resembled adoptive rather than biological parents (Schuett et al 2013).

There has been some discussion whether the effects that mothers have on their offspring's phenotype are necessarily adaptive. Some maternal effects seem to have a clear adaptive advantage either for the mother, the offspring or both (Wells 2007a). While a body of

experimental work implies adaptive advantages to maternal effects (Naett et al 2009) and the term maternal programming is being used increasingly to indicate mother's active preparation of offspring for future circumstances (Weaver et al 2004; Fish et al 2004b; Langley-Evans et al 2005), there are also indications that adaptive advantage cannot be assumed for all maternal effects. For example, maternal exposure to predation risk actually decreases offspring anti-predator behaviour in three-spined sticklebacks (McGhee et al 2012). It has been argued that the information a foetus receives is not in fact about the environment it is likely to face in its lifetime, but rather about the condition of its mother (Wells 2007b). Overall, the adaptive value of maternal effects is strongly ecologically dependent, and can backfire under variable conditions. In such situations, parents may benefit by producing offspring that vary in sensitivity to particular experiences (Frankenhuis and Panchanathan 2011).

### 6.3.3.2 Filial imprinting

Another process which is often overlooked since the initial interest in the 1960s, and which deserves much greater attention both in empirical work and theoretical study, is filial imprinting. It is a process through which young individuals are capable of assimilating information and behavioural strategies necessary for their development (Hoffman and Ratner 1973), even when there is little information available or only for a short time. It has been most studied as the preference of offspring to approach a stimulus to which they have been exposed early in their development (Bolhuis and Honey 1998), and an avoidance of dissimilar stimuli beyond normal avoidance of unfamiliar cues. For example, young male zebra finches preferred a song during which they were exposed during a sensitive period for song learning over their own song, or a new song (Adret 1993). Filial imprinting provides a means for information to be acquired at a time when sensory faculties have not yet developed, through processes different from learning (Ewer 1956), that seem to operate much earlier in ontogeny. Imprinting is expected to be especially relevant for those aspects of development that are sensitive to receiving the correct input on which to base development, for which there is a high cost of failure to receive correct input, and that concerns cues that occur early in the developmental process and are comparatively stable across evolutionary history (Remy 2010). It has been suggested that through imprinting, young can recognise their parents across a variety of conditions, and respond appropriately to a particular posture or movement by a conspecific or predator which they have never seen before (Bateson 1966).

Filial imprinting is based on an ensemble of characteristics presented by the parents (Bolhuis and Honey 1998), rather than on a single attribute or stimulus, and can happen visually, auditory or entirely subconsciously (Bateson 1966). Some of the early work on imprinting indicates that imprinted preferences are surprisingly stable across an individual's

lifetime, even in the face of considerable experience with or even conscious training upon other stimuli (Ewer 1956; Bateson 1966; Salzen and Meyer 1968), and it has been known to affect offspring's behaviour later in life, up to and including their mate choice (Bereczkei, Gyuris, and Weisfeld 2004; Witte and Sawka 2003). Although the exact mechanisms through which juveniles imprint on their parents and others within the social group are still unclear, work in avian biology shows that juveniles are more likely to imprint on more conspicuous cues than less interesting stimuli (Bolhuis and Honey 1998). Great shock among a number of factors has been found to interfere either with the imprinting directly or with the behavioural response given in response (Bateson 1966), although there is also indication that increased stress during development should lead to stronger following and imprinting (Kovach and Hess 1963).

A sub-set of filial imprinting, sexual imprinting, has received more attention and has to date been studied in several species (Irwin and Price 1999), including birds (Witte and Sawka 2003) as well as humans (Bereczkei et al 2004). It has been suggested that sexual imprinting evolved as a mechanism for species recognition (Kozak et al 2011a), although this is still under debate. While not directly linked to coping behaviours, sexual imprinting can help to unravel the mechanisms behind filial imprinting as a whole, and as such can help to clarify important questions like mechanistic reasons as to why children resemble parents.

### 6.3.3.3. Early perceptual learning

Early perceptual learning is any relatively permanent change of perception as a result of experience (Fahle 2004). This process allows individuals to distinguish between similar cues in their environment, for example to differentiate between a dangerous predator and a harmless animal (Brown et al 2011b) or to signal and perceive the identity of intra-group conspecifics (Rendall et al., 1996). It relates to threat and opportunity recognition and the ability to ascertain the correct response to environmental stimuli. As such, early perceptual learning relates to cognition and response estimation as detailed in section 6.2.2.1-6.2.2.2, and subsequently may affect adult behaviour (Beach and Jaynes 1954). Developmentally, perceptual learning seems to rely at least partly on changes on a relatively early level of cortical information processing (Fahle 2004).

Retention of perceptual learning is shaped by a suit of factors such as the strength of initial conditioning as well as individual personality. In a recent empirical study, shy vs. bold rainbow trout showed no difference in conditioned response, but there was a significant effect of personality on retention of learned predator recognition, where shy fish continued to display a conditioned response after 8 days but bold fish did not (Brown et al 2013). In

accord with this study, a low-responsive strain in the same species displayed longer retention of a conditioned response (Øverli et al 2007).

#### 6.3.3.4. Habituation

Habituation is an important process through which individuals tune behaviour to environmental cues. Behaviours developed through habituation originate when animals are exposed to a stimulus continuously or repeatedly and as a consequence decrease their response strength to the stimulus. Habituation to frequently occurring stimuli provides an advantage as it shortens the time needed to estimate a response, and as it prevents unnecessary startle response and activation of defensive or aggressive behaviours.

Habituation has been studied recently especially within the context of response to novelty, as a confounder of experimental values of repeatability or exploration of novel situations. Individual differences in habituation are rarely studied (Martin and Réale 2008). However, rats reared in a social setting showed more rapid habituation to novel objects than rats reared in social isolation, which may account for higher exploration scores in isolated animals (Einon and Morgan 1976). Habituation of minnows to a predator cue was most rapid with the least realistic models (Magurran and Girling 1986), indicating a link between habituation and perceptual learning.

#### 6.3.3.5. Conditioning

Contrary to habituation, which occurs through simple repetition, conditioning occurs when a certain behavioural response is consistently met with positive or negative reinforcement, through which the animal learns to perform this response but not that. For example, hatchery-reared rainbow trout (*Oncorhynchus mykiss*) that were conditioned to recognise chemical predator cues as dangerous, significantly increased anti-predator behaviours (decreased foraging, increased hiding), unlike trout from a control group. This response was still exhibited up to 21 days after conditioning (Brown and Smith 1998). Conditioning can work fast, when it concerns stimuli that are sufficiently harmful, but often works slowly if the negative reinforcement is not very consistent or if the payoff from taking the risk is higher than the cost of negative reinforcement. Like other processes that allow for coping behaviours to be tuned to environmental conditions, conditioning appears to be especially effective early in life. In young male zebra finches (*Taeniopygia guttata*), conditioning with a song as reward influenced the effectiveness of song learning during development but not song preferences in adulthood (Adret 1993). Similar to habituation, there are differences between species and individuals in the way conditions affect behaviour: two closely related species of tadpoles (*Rana lessonae* and *Rana esculenta*) were conditioned for 30 days to a variety of predators, after which species differences were found in the ways general activity

levels and use of refuge changed, as well as differences in the type of predator they responded to (Semlitsch and Reyer 1992).

### 6.3.3.6 Social learning

Social learning includes a wide range of mechanisms through which individuals receive and integrate information from other members of their social group. In humans, children learn social behaviours from their parents through mimicking the role model they provide, through their active parenting style (“this is how our family does it”), and through conditional parenting (“I like you when you follow my values”, see chapter 7). In animals, juveniles learn in very similar ways. What all such mechanisms have in common, is that they involve learning from observation of or interaction with a conspecific (Heyes 1994; Hoppitt and Laland 2008). A special subset of social learning in humans and perhaps some kinds of monkeys is education, where older or more experienced members of the same social group intentionally pass on information, techniques or behaviours to juveniles. Through social learning, animals can acquire more information, skills and behaviours that allow them to deal with their environment than they might reasonably acquire based on personal experience. Social learning also helps juveniles to learn the dominance hierarchy within a group, which facilitates group living and as such the protection provided by a larger group size and the distribution of tasks. A potential disadvantage is that individuals rely on others for the signal they get about environmental conditions rather than relying on their own sensory systems. Social learning is especially common in species where offspring are dependent on their parents for survival for a long time (Schaik 2010), or where they live in strong social groups. Mice, for example, are highly social animals, and young mice reared in a communal nest develop relevant social behaviours that mice reared with single mothers do not (Branchi 2009).

Models of social learning predict that animals living in stable environments should be more attentive to socially acquired information than animals living in variable environments (Zentall and Galef 1988), as under changing conditions, the probability increases that the behaviours of others will reflect past rather than current conditions (Laland 2004). Social learning can be maladaptive when the information modelled by the parents has become outdated with regard to the current environment or when the environment is highly variable (Galef and Whiskin 2004). Models also predict that animals should be influenced more by the behaviour of older than younger group members (Benskin et al 2002). Empirical work on rats supported the first, but not the second of these models (Galef, and Whiskin 2004). Through the development of behavioural patterns within social groups, rearing conditions can have lasting effects on the expression of adult coping behaviours (Rice 2008; Roulin, Dreiss, and Kölliker 2010). Of concern to conservation and coping with challenges of a changing world is recent evidence that wildlife can learn harmful behaviours

## WHY AND HOW THE EARLY-LIFE MATTERS

**Table 6-1** What early-life influences affect the development of animal coping behaviours? Eligible empirical studies addressing effects of early-life influences on animal coping behaviours

Species	Early-life influence	Type	Age	Coping behaviours	Source
prairie vole	parental licking and grooming	2	first 10 days	nurturing, bonding, emotional behaviours, social behaviours	Ahern 2009
rainbow trout	yolk reserves	3	larva at emergence	aggression, social dominance	Andersson 2012
australian tiger snake	habitat	1	1-11 months	habitat choice	Aubret 2008
rhesus macaques	peer-only rearing	4	infant	aggression, play and social behaviour, stress responsivity	Barr 2003
rat	maternal separation	2	pups (days 2-6)	response to novelty, emotional behaviours	Biagini 1998
pig	housing environment	1	birth - suckling	responsivity, maze navigation, behavioural flexibility	Bolhuis 2004
pig	housing environment	1	post weaning	aggression, play and social behaviour, activity	Bolhuis 2005
pig	housing environment	1	suckling	chewing, manipulative and play behaviour	Bolhuis 2006
damselfly	state and predator presence	5	larva stage	activity, boldness, foraging	Brodin 2009
zebrafish	darkness	5	first 6 days	shyness, predator response	Budaev 2009
mallard ducks	immune challenge	5	mid and late development	activity, exploration, response to novelty	Butler 2012
rat	maternal separation and handling	2	first 14 days	response to novelty, exploration, foraging	Caldji 2000
great tit	food availability and sibling competition	3, 4	early rearing	exploration, aggression	Carere 2005
rat	mother's stress	2	gestation	anxiety, maternal behaviour	Champagne 2006
guppy	unpredictability in food supply	3	neonate fry	boldness, exploration	Chapman 2010
mice	communal rearing	4	postnatal	anxiety-like and maternal behaviour, dominance, aggression	Curley 2009
field cricket	conspecific acoustic sexual signals	5	juveniles	aggression and dominance	DiRienzo 2012
killifish	conspecific presence, low food and perceived risk	3, 4, 5	-	exploration, boldness, aggression	Edenbrow 2013
german shepard dog	gender, litter size, season of birth	4, 5	first 10 days	confidence, aggression, physical and social engagement	Foyer 2013
long evens rat	restricted bedding, substitute mother	1, 2	-	anxiety, novelty seeking	Fuentes 2014
rat	litter sex ratio	4	3 days postnatal	aggression, defensive burying, open field behaviour	Gracceva 2011
black-headed gulls	social experience	4	-	aggression, fear, sexual displays	Groothuis 1991
rat	tactile and/or visual stimulation	5	week 1 and 4	passive avoidance reactions	Gschanes 1998
cavies	Photoperiod	5	-	exploration, boldness, stress response	Guenther 2013
mice	threat of infanticide	2	-	anxiety and exploration	Heiming 2009
rabbit	relations with siblings	4	littering	behavioural style, stress response	Hudson 2011

Species	Early-life influence	Type	Age	Coping behaviours	Source
spotted skiffia	habitat	1	rearing	courtship, aggression, boldness, foraging	Kelley 2005
guinea pig	social instability for mothers	2	gestation	dominance, courtship, reactivity	Kemme 2008
zebra finch	nutritional conditions	3	nestling / fledgeling	exploration, foraging, sensitivity to food restriction	Krause 2009
chimpanzee	social and maternal isolation	2, 4	infant	activity, abnormal behaviour	Martin 2002
cat	socialisation and father's behaviour	2, 4	week 2 to 12	response to familiarity and novel objects, boldness	McCune 1995
hose	maternal separation	2	week 2 to 12	stress behaviours	Moons 2005
zebrafish	habitat	1	from birth	shoaling, activity, boldness, foraging, aggressiveness	Moretz 2007
zebrafish	social experience with dissimilar fish	4	juveniles	aggression, boldness, activity, stress behaviour	Moretz 2007
great tit	social group size	4	nestling	stress response, exploratory behaviours	Naguib 2011
field cricket	population density	4	nymphal stage	boldness, aggression	Niemela 2012
rat	postnatal handling	2	first 21 days	reactivity to novelty and conflict	Nunez 1996
pike	body size and growth	5	-	foraging behaviour across risk/boldness	Nyqvist 2012
dog	audiovisual playbacks	5	week 7 and 8	exploration, fearfulness	Pluijmakers 2010
salmon	environmental enrichment	1	rearing	risk taking behaviour	Roberts 2011
rat	body mass and litter size	4	-	boldness, exploration, anxiety	Roedel 2011
rabbit	body weight	3	early postnatal	anxiety, exploration	Roedel 2011b
rat	postnatal isolation	2	first 14 days	escape and avoidance	Ruedi-Bettschen 2004
stickleback	Predation	5	-	boldness, aggression	Sih 2007
rat	mother isolation	2	days 2-10	activity, orienting, risk taking	Spivey 2008
spider	habitat	1		boldness, foraging aggression	Sweeney 2013
rat	social isolation	4	day 23-38 (post weaning)	social recognition, anxiety	Tanaka 2010
mustard leaf beetle	environmental food conditions	3	-	boldness, activity, exploration	Tremmel 2013
pig	isolation	4	day 3-11	coping with endotoxin, suckling behaviour	Tuchscherer 2006
rat	isolation	4	week 4 and 5	social behaviour, ambulation, rearing, self-grooming	van der Berg 1999
cow	mother vs. artificial rearing	2	first 90 days	vigilance, escape, play and social behaviour	Wagner 2013
rat	environmental bacteria	5	day 3 and 5	anxiety-like behaviour	Walker 2004
cleaner wrasse	habitat social complexity	4	-	cooperation and cognition	Wisner 2014

Environmental influences are categorised as habitat (1), parenting (2), nutrition (3), social environment (4) or other influences (5).



from each other: whether or not bottlenose dolphins (*Tursiops aduncus*) become conditioned to being illegally fed by recreational fishers depended on both the degree to which the dolphins would frequent high tourist areas, and the degree to which they associated with previously conditioned dolphins (Donaldson et al 2012). This also shows a relationship between conditioning and social learning.

### 6.3.4 Early-life influences on coping

In answer to question 2, search terms yielded 64 different mentions of early-life influences on coping behaviours, 52 of which from empirical studies (see table 6-1). Most prevalent in these studies were effects stemming in some way from the parents, either directly through parenting efforts, or indirectly through parent's choice of rearing territory. From these 52 studies, we distilled four most important early-life influences: habitat conditions (studied in 9 studies), parents (14 studies), nutrition (7 studies), and social environment (18 studies), which we discuss in more detail hereafter. Other important early-life influences (11 studies) are abiotic factors such as photoperiod and season of birth, as well as direct influences to physical health such as predation, environmental bacteria and immune challenges.

Stress appears to be a relevant detrimental influence across all of these categories, whether it concerns stress from maternal separation, lack of nutrition or unpredictable nutrition, bacterial infection or social difficulty. Rather than a separate type of early-life influence, stress represents unfavourable conditions beyond what the animal's biology can easily cope with and can occur in many variations.

#### 6.3.4.1. Habitat

Within eligible studies, effects of early-life habitat conditions were studied by means of habitat (Kelley et al 2005; Moretz et al 2007a; Aubret and Shine 2008; Sweeney et al 2013), housing environment (Bolhuis et al 2004; Bolhuis et al 2005; Bolhuis et al 2006), restricted bedding (Fuentes et al 2014) and environmental enrichment (Roberts et al 2011).

Most interest in effects of early-life habitat is based in the question how laboratory and housing conditions affect animal's coping style. Laboratory-reared fish (*Skiffia multipunctata*) displayed increased courtship, aggression and curiosity towards a novel predator compared to pond-reared fish, and commenced foraging on novel food more rapidly (Kelley et al 2005). Laboratory-reared spiders (*Penultimate A. pennsylvanica*) never exhibited a behavioural syndrome between boldness and foraging aggressiveness, while field-reared penultimates (but not juveniles) did (Sweeney et al 2013). Early-life housing conditions were also shown to affect coping behaviours in pigs (*Sus domesticus*): barren housed pigs were less active, less explorative, less playful, and showed more social aggression than pigs raised in enriched housing (Bolhuis et al 2005). Similarly, pigs from enriched housing were show to have more difficulty responding to changes in a spatial

discrimination maze than pigs from barren housing (Bolhuis et al 2004), behaviour which relates to their ability to cope with changes in foraging conditions. Housing conditions did not affect all individuals equally: low-resisting pigs more were more affected by adverse housing than high resisting pigs across various behaviours, including chewing, manipulative and play behaviours (Bolhuis et al 2006). In rats, behavioural effects due to restricted bedding during the first days after birth (in addition to another early life stressor), was show to affect males and females differently depending on measured behaviours (Fuentes et al 2014). For a more extensive review, see chapter 5.

In a more ecological setting, snakes (*Notechis scutatus*) were found to base habitat choice, an important life history decision that affects coping success in many aspects of life, on the habitat type in which they had been reared – an adaptive effect as they were also found to be more effective in locomotion in these habitats than in others (Aubret and Shine 2008). Fine-tuning behaviours to the early-life habitat provides a benefit when conditions experienced as juveniles are likely to match conditions in later life.

Such effects of habitat and housing conditions experienced early in life are especially important with regards to experimental design of animal behaviour studies, but are also interesting in relation to studying behavioural plasticity and animal's ability to adapt to shifts in habitat quality or size.

#### 6.3.4.2 Parents

In many of the studies we reviewed, the role of the parents is extensive. Parents affect their offspring through genetics, through the security and nutrition they provide, through the example they set, through their parenting behaviours such as grooming and licking, and the behaviour they actively encourage in their offspring. In addition, mothers affect their offspring through of hormonal influences (Dufty Jr et al 2002; Weaver et al 2004; Champagne 2011) during gestation. While some studies include parent-child interactions in their definition of social interactions, as juveniles learn important behavioural systems from both parents and others in their social group, for purpose of this study we consider them separate influences in order to clarify effects unique to the parent-child relationship. Within eligible studies, parenting was studied especially during the last decade in the context of maternal isolation (Biagini et al., 1998; Caldji et al., 2000; Martin, 2002; Moons et al., 2005; Ruedi-Bettschen et al., 2004), and more recently maternal stress (Champagne and Meaney 2006), which has often been related to intergenerational effects (see section 6.3.5).

Many studies found detrimental effects of maternal separation early in life. For example, rats separated from their mothers early in life displayed reduced activity and risk taking, and increases in orienting time (Spivey et al 2008), while other rats showed impaired

coping (Ruedi-Bettschen et al 2004). Calves (*Bos primigenius*) reared by mothers showed more escape and vigilance behaviour than automat-reared cows when faced with an isolation test, and displayed overall more social behaviours towards conspecifics (Wagner et al 2013). In addition, chimpanzees (*Pan troglodytes*) separated from their mothers and/or social group as juveniles showed decreased activity and increased abnormal behaviours, with stronger effects in younger individuals (Martin 2002). Other studies found an effect of early postnatal handling but not of maternal separation on the ability of juvenile rats to cope with novelty (Biagini et al 1998), and adult rats who had been handled as juveniles showed reduced startle responsivity, increased exploration and decreased suppression of feeding whereas those that were maternally separated as juveniles did not (Caldji et al 2000). Such effects of handling (see also (Nunez et al 1996; Spivey et al 2008) indicate that separation and handling cannot be considered comparable influences, and call for caution when studying effects of parental separation.

Interestingly, some studies have looked at parental behavioural traits in relation to offspring coping, showing that juvenile cats from friendly fathers were quicker to approach, touch and rub an unfamiliar person and remain in close contact with novel objects than those from unfriendly fathers (McCune 1995). Similarly, offspring of exploratory zebrafish females were always highly exploratory regardless of behavioural traits of the father (Wisenden et al 2011). No differences were found between coping behaviours of guinea pigs whose mothers experienced a socially unstable environment vs. those who experienced stable social conditions (Kemmer et al 2008).

#### 6.3.4.3. Nutrition

## 6

Nutrition is perhaps the most important building block for development of the physical body. More recently, it has also been linked to the development of behaviour, which can be understood adaptively as a result of early-life environmental cues indicating to juveniles that their surroundings are scarce in food availability, and that an adjustment of developmental pathways governing foraging behaviours is required. If scarcity of food leads to slower growth rates and smaller size, other behavioural processes may need to be adjusted to the situation as well. In addition, lack of appropriate nutrition affects the mechanics of developmental systems, potentially stunting or derailing healthy development. Selected papers studied the effects of yolk reserves (Andersson and Hoglund 2012), food availability (Carere et al 2005; Edenbrow and Croft 2011), food quality (Krause et al 2009; Tremmel and Müller 2012), and body weight (Roedel and Monclus 2011).

Female zebra finches (*Taeniopygia guttata*) raised on low quality food were faster to show exploration and foraging behaviours than those raised on high quality food, although there were no differences in latency to move after start of experiments (Krause et al 2009).

Young trouts (*Oncorhynchus mykiss*) with larger yolks showed more aggressive personality traits than siblings with smaller yolks, and subsequently were more aggressive in territory establishment and more socially dominant (Andersson and Hoglund 2012). However, in a line of great tits selected for fast exploration (*Parus major*) food rationing was linked to increased aggression (Carere et al 2005), and in a different species of fish (*Kryptolebias marmoratus*), low food conditions reduced exploration but not boldness or aggression (Edenbrow and Croft 2011). In a species of beetle (*Phaedon cochlaeriae*), low-quality food induced boldness, and by extension, potential foraging success, while animals raised on high-quality food were more active (Tremmel and Müller 2012). These studies indicate that effects of nutrition do influence adult coping behaviours, but not all behaviours or in the same way. Negative consequences of food deprivation during ontogeny may reappear especially when environmental conditions deteriorate in adulthood (Krause et al 2009).

#### 6.3.4.4. Social environment

The relationship between individuals and a group of conspecifics is often referred to as their social environment, which especially in recent years has been an increasingly popular topic in animal behaviour. The social environment is important in processes of social learning (see section 6.3.3.6), but also relates to safety from predators for animals living in groups, and competition for resources. Within selected studies, effects of early-life social environment were studied quantitatively in the context of early-life social isolation (Van Den Berg et al 1999; Tuchscherer et al 2006; Kemme et al 2008; Tanaka et al 2010) on one hand and group size (Roedel and Meyer 2011; Naguib et al 2011a; Edenbrow and Croft 2011; Niemela et al 2012) on the other, and qualitatively in the context of relationships with siblings and other conspecifics (Carere et al 2005; Moretz et al 2007a; Hudson et al 2011; Wismer et al 2014).

Juvenile isolation from a social group was found to affect development of social behaviours in rats, in frequency, duration and latency of various social behavioural elements such as social exploration, approach/following and anogenital sniffing. However, when social contact was initiated, a relatively normal behavioural pattern was displayed (Van Den Berg et al 1999). Other studies found that socially isolated juvenile rats had difficulty with social recognition (Tanaka et al 2010). In rodent species like rats and mice, social environment can be studied through the communal nest (CN), an experimental setting based in rodent natural nesting behaviour in which juveniles can interact with peers as well as with their mother and sibs (Branchi 2009). Communally reared offspring were found to display reduced anxiety-like behaviour when exposed to novel environments, and females were more subordinate and less aggressive when exposed to an intruder male (Curley et al 2009).

Litter size affected anxiety in rats in a nonlinear way: young rats born to small or large sized litters had higher scores of anxiety-like behaviours than those from medium-sized litters (Roedel and Meyer 2011). Group size also affected aggression, fear and display behaviours in black-headed gulls (*Larus ridibundus*), which was not reversed after birds were re-housed in larger groups (Groothuis and Mulekom 1991).

An interesting study into the effects of housing different strains of zebrafish (*Danio rerio*) together as juveniles, showed an increased willingness to leave the vicinity of a shoal compared to juveniles raised in a pure strain, but found no effects on activity, predator response or stress recovery (Moretz et al 2007b). A review on rabbits, rats and mice showed that early sibling relations, such as position in the little huddle, contributed to the development of individual differences in behavioural style (Hudson et al 2011).

### 6.3.5 Intergenerational transmission of coping behaviour

A discussion on the processes through which early-life influences affect the development of coping behaviours is not complete without considering how environmental experiences during ontogeny of one generation affect the expression of phenotypes in the next generation (Champagne 2010; Moran et al 2010), and how such early-life influences can lead to transmission of coping skills from one generation to the next, a phenomenon commonly known as intergenerational (Conger et al 2009) or transgenerational (Matthews and Phillips 2010) effects. In the literature, there exists a confusing overlap in terminology between maternal effects (see section 6.3.3.1) and intergenerational effects. To mediate this confusion, we define intergenerational transmission as non-genomic effects in which a particular phenotypic expression is transmitted from one generation to the next, whereas maternal effects can be considered simply the effects of maternal phenotype on offspring phenotype. Following this, a juvenile that grows stronger because its mother has a high status and can provide better nourishments is an example of maternal effects, and a juvenile who has a high status in the group because its mother has a high status is an example of intergenerational effects. Similarly, using an example cited earlier, cases where offspring experience behavioural disorders linked to maternal smoking during pregnancy (Abbott and Winzer-Serhan 2012) constitute maternal effects, while cases where offspring suffer from a smoking addiction due to maternal smoking during pregnancy (Hellstrom-Lindahl and Nordberg 2002) should be considered intergenerational transmission of coping. Maternal effects, just like other mechanisms affecting early life, concern input and response: due to this early-life influence, that later-life phenotype developed. Intergenerational effects concern heritability: due to the previous generation having a certain phenotype, the next generation has a similar phenotype. Clearly, there will be some overlap, as maternal effects and other early-life influences can lead to intergenerational effects (Broadhurst 1961). The distinction is important, however, because the two

processes have different implications both for evolutionary theory and child development models (Herman et al 2014).

In answer to question 3, nine empirical studies specifically showed parenting behaviours that affected the coping behaviour of subsequent generations, through maternal example and care, lack thereof, or abuse thereof. Within the included studies, all studies discussed effects relating to mothers, and only one related to both parents (Schuett et al 2013).

Many studies concerning intergenerational transmission are conducted in rodents on the topic of parental care. There is increasing evidence that environmental effects experienced even before conception can be transmissible to subsequent generations (Burton and Metcalfe 2014). For example, dams who were exposed to chronic social stress displayed impaired maternal care to F1 offspring, who in turn displayed impaired maternal care to F2 offspring. Both male and female offspring displayed decreased social behaviour (Babb et al 2014). Similarly, mouse dams rearing pups in communal nests displayed increased maternal care, to which their F1 offspring displayed reduced anxiety-like behaviour when placed in a novel environment, and increased quality of parenting behaviours towards their own offspring. F2 offspring also displayed reduced anxiety-like behaviour and better parenting (Curley et al 2009). An elegant early study in monkeys showed that the amount of contact mothers had with their offspring was related to the amount of contact they themselves had with their mothers. In this, a female's experience in infancy was a better predictor of adult mothering than variables such as social learning as a juvenile, shared circumstances and average similarity between mothers and daughters (Fairbanks 1989).

Intergenerational effects do not just express in parenting, however. Hypo-responsiveness to stress across several behavioural categories was shown in macaques whose mothers had been exposed to early-life stress, even when those mothers no longer displayed hypo-responsiveness themselves anymore (Kinnally et al 2013). Abusive behaviour as well was shown to transmit across generations: nine of 16 female rhesus monkeys who were abused by their mothers during their first month of life displayed abusive parenting with their firstborn offspring, regardless of whether they were reared by their biological mother or a foster mother (Maestripietri 2005). Interestingly, exploratory type of young zebra finches (*Taeniopygia guttata*) was predicted by the exploratory behaviour of their foster parents, but not by that of the genetic parents, or other social influences such as rearing regime, hatching position, brood size or gender (Schuett et al 2013).

**Table 6-2** *How do coping behaviours of the parents transmit to their offspring through early-life influences?*

<b>Species</b>	<b>Age</b>	<b>Parental influence</b>	<b>Coping behaviours</b>	<b>Author, year</b>
<b>rat</b>	lactation	chronic social stress (f0), impaired maternal care (f1)	maternal care (f1), social behaviour (f2)	Babb 2014
<b>rat</b>	gestation	stress	maternal licking and grooming	Champagne and Meaney 2006
<b>mice</b>	postnatal	communal rearing	anxiety-like and maternal behaviour, dominance, aggression	Curley 2009
<b>vervet monkeys</b>	first 6 months	mother-child experiences	mothering behaviours	Fairbanks 1989
<b>domestic chicken</b>	first 3 weeks	stress by social isolation	correct choices in learning test	Goerlich 2012
<b>quail</b>		habitat hiding spaces	emotional and social reactivity of offspring	Guesdon 2011
<b>rhesus monkey</b>	first 1 month	maternal abuse	abusive parenting	Maestripieri 2005
<b>stickleback</b>	-	maternal predator exposure	response to predator	McGhee 2012
<b>zebra finch</b>	-	parental personality	exploratory type	Schuett 2013

Although of course the mechanisms leading to intergenerational transfer of behaviours and coping traits consist of a complex interplay between ecological and physiological factors (Wells 2011), of the processes linking early-life environment to development as discussed in section 6.3, maternal effects and imprinting are likely to be the most important in generating intergenerational effects (see Table 6-2). And indeed, we find many examples in the literature of cases where such processes affect coping in juveniles (Mousseau and Fox 1998; J. Marshall and Uller 2007; Agrawal, Brodie, and Brown 2001; Moran, Dias, and Marshall 2010), although more attention has been paid to maternal effects than to imprinting (Champagne 2011; Drake et al 2011). The early-life influences responsible, following recent literature, are most likely to be social and reproductive behaviour and stressors experienced in these areas (Champagne 2010), although there appears to be somewhat of a bias in the literature towards studying mainly maternal influences (Champagne and Meaney 2006) on offspring social and emotional behaviour, and mainly in rodents and primates.

## 6.4. Stable or stuck?

Perhaps one of the most important environmental challenges for both animals and humans to cope with is change. Changes in the environment are especially unsettling because they require animals to respond in new, different ways, with no guarantee that the response they select will be functional. Given the strong effects of the early-life environment to shape a multitude of behaviours and coping skills later in life, we have to ask the question: in our current radically and fast changing environment, do our early life experiences help to create stable behaviours and coping skills, or do they leave us stuck in the past?

While developmental processes have formed over evolutionary time through survival of those young animals who most effectively responded to environmental pressures, such processes and the ways they are influenced by environmental factors should not be considered necessarily adaptive in their own right, but are simply proximate causes that affect later-life coping. As such, under changing conditions, processes that have provided an advantage for juveniles throughout evolutionary history may suddenly become disadvantageous. In addition, developmental processes for many animal species may not be equipped to acquire accurate information about or under novel environmental conditions, such as street lights and urban noise (Miranda et al 2013b).

Important concepts when discussing the adaptive advantages and disadvantages that come with sensitivity of developmental processes to early-life conditions are resilience and reversibility. Resilience, the capacity to recover from difficulties, is important in estimating the strength with which negative experience continues to influence. Reversibility relates to the ability to reverse or undo the effects of (harmful) environmental conditions, and is especially important once coping behaviours have been established yet found unfavourable, or when the conditions on which their development was based have changed. While adaptation to early-life conditions can clearly be an adaptive mechanism, the ability to reverse the effects of early-life environments seems equally adaptive especially in the case of improved conditions or changed environments from infancy to adulthood.

Although some negative influences of the early-life environment have been shown to be reversible, this reversibility does not appear to apply to all affected coping behaviours. While there is evidence that beneficial later-life circumstances can partially remedy or even completely negate developmental limitations (Salzen and Meyer 1968; Francis et al 2002; Gabriel 2005), there is also evidence that negative experiences during development continue to negatively affect behavioural functioning for the entire lifespan of an individual (Champagne 2010). For example, female cichlids, if raised in poor conditions, would raise larger young even after experiencing rich conditions during all of adulthood (Taborsky 2006). In part, this seems to be linked to the timing of the negative influence. For example,



there is indication that the earlier children experience adversity, the more likely they are to develop antisocial personality problems (Keiley et al 2001). Reversibility of early-life damage such as stress experienced by either mother or child has been shown in mice (Curley et al 2009), rats (Champagne et al 2003; Cui et al 2006) and humans (Keay and Bandler 2001; Francis et al 2002). Reversibility of imprinting on early-life stimuli, however, seems to be much harder as imprinted behaviours appear quite stable throughout later life even with extensive training upon other stimuli (Salzen and Meyer 1968). As the processes of early perceptual learning, habituation and conditioning as such have not received much attention, little is known as to the differences between these processes in resilience and reversibility. However, reversibility of the effects that social learning has on coping behaviours have been studied to greater extent, and effects of maternal separation and social deprivation have been shown to be reversible in some species, and some situations. For example, for young chimpanzees who grew up without their mother or without conspecifics at all, recovery of healthy behaviours may occur with access to an enriched social environment (Martin 2002).

In some cases, especially when environmental conditions impact developmental processes that occur early in ontogeny or canalisation, negative behavioural consequences of environmental influences may not be reversible. In such a case, the individual finds itself stuck with the coping strategies developed during early-life and may suffer fitness consequences. For example, cross-over studies in animals suggest that exposure to adversity in early life does not necessarily increase fitness in tough adult environments. Rather, those malnourished in early life do worse in adult environments, but particularly so in tough adult conditions (Reid et al. 2006; Taborsky 2006a).

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In other cases, however, effects of early-life conditions, even when they have been carried over across many generations, may still be reversed. For example, the Balb-C mouse strain is often considered “socially-incompetent” and anxious, yet when young of this strain were reared in a communal nest instead of under regular laboratory conditions, anxiety-like behaviours and parental care were improved in both first and second generation offspring (Curley et al 2009). Results such as these imply that the harmful coping behaviours in this strain may be a result of intergenerational effects of standard housing conditions, which can be attenuated both within and across generations in cases where sufficient reversible. This example from animal models is encouraging, and may be applied in other species, including humans.

### 6.5. Discussion

The purpose of this review was to integrate ultimate and proximate causes of early-life influences on the development of coping behaviours. To our understanding, this is the first review to attempt combining early-life influences with the processes through which coping

behaviours are established. Meta-analysis yielded comparatively few papers that specifically addressed developmental processes, and the majority of those addressed epigenetic mechanisms and parental effects. As previously indicated by several recent articles (Stamps and Groothuis 2010; Gracveva et al 2011; Groothuis and Trillmich 2011b), the relationship between external events and individual's resulting coping behaviours has been surprisingly understudied. Individual developmental processes, such as maternal effects, imprinting, habituation, conditioning or social learning, have been well studied for decades across fields of animal ecology, neurology and psychology, but with the exception of maternal effects, have not been studied in context of the development of coping behaviours.

The reason for the lack of a framework for developmental processes becomes clearer when reviewing the large number of coping behaviours studied in the literature, and the diversity of early-life conditions: a multitude of behavioural aspects, the correlations between which are still poorly understood, are influenced by an equally large number of environmental conditions in sometimes opposite directions, with important differences between and within species and even individuals. As different fields of study each have their preferred study species, environmental conditions and coping behaviours, comparing the available studies and constructing a bigger picture poses a challenge. Especially for that reason, however, there is a need to study and uncover the pathways through which early-life condition affect coping, so that a linear "this condition leads to that expression" can be replaced with a deeper understanding of the development of behavioural patterns. We recommend more targeted studies that focus less on relating an environmental influence to a behavioural expression, and more on the functioning of processes through which individuals ascertain and integrate external information and translate this information to behavioural patterns. We expect that such an approach will shed light on inconsistencies currently reported in this field (Moons et al 2005) as proximate causes are better understood. Such understanding will be especially useful in relation to resilience and reversibility of unfavourable traits, both of which are becoming increasingly important at the moment as most species, including humans, are challenged with large amounts of environmental change.

Not all environmental influences are equally important, or affect development equally throughout all years of infancy. Adaptively, it doesn't make sense that it would, and mechanistically, it doesn't seem feasible that it could. Sensitive stages in early-life, during which juveniles are especially vulnerable to maltreatment, stress or deprivation of important stimuli, occur mainly due to maturation of developmental pathways (Rao et al 2010). During childhood and adolescence, the brain structures involved in coping behaviours have different maturation pathways and as a result each structure has specific sensitive periods for exposure to stress (Lupien 2009), and other input. When the

underlying neurochemistry of behavioural structures does not develop early in life, such behaviours often do not develop later in life or develop only partially. Language is a well-studied example of this: the initial rate of language acquisition and the ultimate level of attainment depend at least partially on the age at which learning begins, while outside the sensitive period for language development, acquisition is irregular and incomplete. This has been linked to a loss of neural plasticity and differs between individuals (Long 1990). Although sensitive periods are largely a property of neural circuits, they are reflected in behaviour (Knudsen 2004). Behaviours developed early in life can generally be applied later in life, but not all behaviours can be developed later in life. Often the pre-existing conditions simply do not exist or have developed (canalised) into a different direction. Alternatively, damage may have been done early in development that prohibits development in a certain direction.

When considering sensitive stages in the development of coping behaviours, there is a need to distinguish between two different, though perhaps partially overlapping factors: sensitivity to receiving the necessary input (Bolhuis and Honey 1998; Zala et al 2012), and sensitivity to negative influences such as stress or malnutrition (Krause et al 2009; McClelland et al 2011). Developmentally, these factors affect different parts of the growing individual: the input necessary for healthy development of coping behaviours that benefit the juvenile throughout their life should be a consistent, reliable stream of information pertaining to the (social) environment that juveniles are growing up in and is most important while the individual is developing the underlying neurochemical pathways. Deprivation of such necessary input during the sensitive stage may mean the juvenile will never develop the appropriate behaviour. Negative influences, on the other hand, can consist of (but not be limited to) momentary disruption of a developmental pathway, and as such not necessarily be limited to a sensitive stage. For this reason, early life stress (ELS, Fuentes 2014) should be considered within context of the stressor, as evolutionary speaking, insufficient or abusive maternal care cannot be easily equated to lack of nutrition or lack of social interaction with conspecifics.

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