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The other facets of family life and their role in the evolution of animal sociality

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ABSTRACT

Family life forms an integral part of the life history of species across the animal kingdom and plays a crucial role in the evolution of animal sociality. Our current understanding of family life, however, is almost exclusively based on studies that (*i*) focus on parental care and associated family interactions (such as those arising from sibling rivalry and parent-offspring conflict), and (*ii*) investigate these phenomena in the advanced family systems of mammals, birds, and eusocial insects. Here, we argue that these historical biases have fostered the neglect of key processes shaping social life in ancestral family systems, and thus profoundly hamper our understanding of the (early) evolution of family life. Based on a comprehensive survey of the literature, we first illustrate that the strong focus on parental care in advanced social systems has deflected scrutiny of other important social processes such as sibling cooperation, parent–offspring competition and offspring assistance. We then show that accounting for these neglected processes – and their changing role over time – could profoundly alter our understanding of the origin and subsequent evolution of family life. Finally, we outline how this 'diachronic' perspective on the evolution of family living provides novel insights into general processes driving the evolution of animal sociality. Overall, we infer that the explicit consideration of thus-far neglected facets of family life, together with their study across the whole diversity of family systems, are crucial to advance our understanding of the processes that shape the evolution of social life.

Key words: family life, parental care, group-living, evolutionary transition, sociality, precocial, altricial, parent–offspring conflict, sibling rivalry, sexual conflict.

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I. INTRODUCTION

Social life in family groups is a highly variable phenomenon that is widespread across the animal kingdom. Family groups can be found in vertebrates such as mammals, birds and (non-avian) reptiles, as well as in numerous invertebrates including arthropods, molluscs and annelids (Clutton-Brock, 1991; Trumbo, 2012; Wong, Meunier & Kölliker, 2013). Both within and across these taxa, families can vary tremendously in terms of composition, persistence and intimacy of social interactions (Klug, Alonso & Bonsall, 2012; Trumbo, 2012). For instance, family groups can be composed of one or multiple offspring and either their mother, their father, or both parents; they can last from only a few hours to an entire lifetime; and they can range from temporary and facultative aggregations over cooperatively breeding groups to highly integrated eusocial societies featuring reproductive division of labour (Hölldobler & Wilson, 1990; Costa, 2006; Koenig & Dickinson, 2016).

The emergence of family life is commonly thought to constitute a transition from solitary to social life, and marks the initial step in the 'major evolutionary transition' to eusociality (Maynard Smith & Szathmáry, 1995; Bourke, 2011). In particular, the origin of family life entails the emergence of a novel social environment (see Badyaev & Uller, 2009; Uller, 2012) that can become an integral part of an organism's life history (Clutton-Brock, 1991; Gross, 2005; Wong *et al.*, 2013), and may create long-lasting bonds between parents and their offspring. Such bonds preceded the evolution of many derived social behaviours (Darwin, 1871; Wilson, 1975; Royle, Smiseth, & Kölliker, 2012*b*), and thus likely drove the transformation of simple family systems to advanced animal societies. Eusocial societies, for instance, likely arose from family units in which offspring delayed dispersal and independent reproduction, and instead assisted their parents in raising younger siblings (Boomsma & Gawne, 2018). Studying family life can thus help to

elucidate factors that shape the evolution of complex animal societies (e.g. Wheeler, 1928; Michener, 1969; Wilson, 1975; Bourke, 2011), and more generally shed light on mechanisms that commonly promote the emergence and maintenance of social life in nature.

Despite its crucial role in social evolution, the origin and maintenance of family life surprisingly is often only touched upon indirectly in studies focusing on parental care (but see, for instance, Falk *et al.*, 2014; Jarrett *et al.*, 2017). Parental care is a core feature of family life, since family groups typically arise where parents extend existing forms of care beyond offspring hatching or birth (e.g. Lack, 1968; Clutton-Brock, 1991; Smiseth, Kölliker & Royle, 2012). It comprises a variety of traits ranging from gamete provisioning through nest construction to brood attendance and food provisioning (reviewed in Clutton-Brock, 1991; Costa, 2006; Smiseth *et al*., 2012; Wong *et al.*, 2013), and generally encompasses "any parental trait that enhances the fitness of a parent's offspring, and that is likely to have originated and/or to be currently maintained for this function" (Smiseth *et al.*, 2012, p.7). The expression of care often has a large impact on the fitness of both parents and offspring. In particular, parental care is beneficial to offspring, because it increases their quality and/or survival by neutralizing environmental hazards (Alonso-Alvarez & Velando, 2012; Klug & Bonsall, 2014). By contrast, parental care is often costly to parents, because it can reduce their condition and/or survival (for instance as the result of increased energy loss or elevated risk of predation), and may thus ultimately diminish their lifetime reproductive success (Trivers, 1972; Alonso-Alvarez & Velando, 2012). Shedding light on the circumstances that allow family members to gain sufficient benefits to offset these direct costs (Hamilton, 1964; Smiseth *et al.*, 2012) has thus long been considered central in the study of family life (Clutton-Brock, 1991; Gross, 2005).

However, parental care is but one of many facets of family life and only a fraction of the other facets has received scrutiny to date. For instance, it is well known that the expression of care can prompt evolutionary conflicts (Parker, Royle & Hartley, 2002; Royle, Hartley & Parker, 2004) that become apparent (*i*) if one parent tries to reduce its parental investment at the other parent's expense (sexual conflict; Trivers, 1972; Lessells, 2012; Parker *et al.*, 2015); (*ii*) if offspring compete with each other for limited parental resources (sibling rivalry; Mock & Parker, 1997; Roulin & Dreiss, 2012); and (*iii*) if offspring demand more care than the parents are willing to provide (parent–offspring conflict; Trivers, 1974; Kilner & Hinde, 2012; Kölliker *et al.*, 2015). By contrast, processes such as sibling cooperation and parent–offspring competition have only recently started to attract attention (e.g. Dreiss, Lahlah & Roulin, 2010; Yip & Rayor, 2013; Falk *et al.*, 2014; Schrader, Jarrett & Kilner, 2015*a*; Kramer *et al.*, 2017). This disparity arguably results from a strong bias towards studying family interactions in the derived social systems of birds and mammals [see Clutton-Brock (1991), Roff (1992), Stearns (1992) and Balshine (2012) for reviews]. In these groups, young offspring are completely dependent on parental resources, and the substantial fitness effects of parental care that parallel this dependency typically prompt intense conflicts over the allocation of care (Clutton-Brock, 1991; Gross, 2005). Derived family systems, however, only represent a small fraction of the diversity of family life in nature. Their predominance in empirical studies thus has promoted (and was reinforced by) the development of an incomplete theory of family life that neglects mechanisms playing a greater role in less-derived family systems (see also Costa & Fitzgerald, 1996). Moreover, the central role of parental care arguably deflects scrutiny of fitness effects that are typically masked by the benefits and costs of (conflicts over the allocation of) parental care. The strong focus on parental care and its expression in derived social systems hence likely distorts our understanding of the mechanisms driving the

emergence and subsequent evolution of family life and could ultimately obscure their role in the (early) evolution of animal sociality.

Here, we advocate a comprehensive framework for the study of family life that integrates the (changing) role of all types of family interaction in elucidating the evolution of animal sociality. To this end, we (*i*) illustrate the downsides of a narrow focus on parental care by reviewing how thus-far neglected types of family interaction can shape the cost–benefit ratio of family life. We then (*ii*) outline how accounting for these overlooked mechanisms – and their changing roles over time – could improve our understanding of the origin and subsequent evolution of family life. Finally, (*iii*) we discuss how this 'diachronic' perspective (see Section IV) on the evolution of family living could provide general insights into the mechanisms driving social evolution. Overall, we infer that understanding the evolution of family life requires a complete picture of all factors that affect its fitness consequences across taxonomic groups. While doubtless very important, parental care and its repercussions in advanced family systems only cover part of the canvas.

II. THE SEMANTICS OF FAMILY LIFE

Somewhat surprisingly, there is no strict consensus among behavioural ecologists as to what constitutes a family. In studies on cooperative breeding, the term 'family' is typically restricted to cases where mature offspring forgo dispersal and independent reproduction, and instead continue to interact regularly with their parents (Emlen, 1994, 1995; Covas & Griesser, 2007; Drobniak *et al.*, 2015). This narrow definition helps to identify transitional stages in the evolution of cooperative breeding (a form of family living characterized by reproductive cooperation; Drobniak *et al.*, 2015). Yet, this definition also excludes the vast diversity of (less-enduring) associations between parents and their immature offspring. A broader meaning of the term 'family' is thus

frequently implied in studies on parental care (see Clutton-Brock, 1991; Gross, 2005; Schrader *et al.*, 2015*b*; Duarte *et al.*, 2016; Jarrett *et al.*, 2017). Here, we formalize this view by defining a family as an association of one or both caring parent(s) with their offspring after hatching or birth that arose and/or is currently maintained to enhance the fitness of the constituent individuals. This broad definition closely matches the colloquial meaning of the term family and allows us to outline a general perspective that covers all types of (non-random) parent–offspring association. We suggest using more narrowly defined terms such as 'nuclear family' and 'extended family' to delineate families of a particular composition. Specifically, we propose to use the term 'nuclear family' to delineate the vast majority of family systems that consist of one or both caring parent(s) and offspring of a single reproductive attempt. Conversely, we suggest using the term 'extended family' to delineate families consisting of a nuclear family and their close relatives, such that the extended family also comprises grandparents, siblings of the parents, and/or offspring of at least one additional reproductive attempt. Many societies of cooperatively breeding birds, mammals, and eusocial insects are examples of such extended families.

Family systems may not only differ in terms of composition, but also in terms of the juveniles' developmental mode. This latter difference is captured by the classification into species with altricial and precocial young (henceforth referred to as altricial and precocial species, respectively). In altricial species, juveniles are born in an immature state, and thus cannot survive without receiving at least some care early during their life (Starck & Ricklefs, 1998). Family life in altricial species – including many mammals, as well as all passerine birds and eusocial insects – is therefore always obligatory (Clutton-Brock, 1991). In precocial species, on the other hand, juveniles are born in a relatively mature state, and can survive in the absence of (nonetheless beneficial) care due to early development of their capability to forage independently (Starck &

Ricklefs, 1998). Family life in precocial species – including ducks, plovers, quails and many subsocial insects – is therefore often facultative (Smiseth, Darwell & Moore, 2003; Kölliker, 2007).

Intriguingly, these differences in the family life of altricial and precocial species likely reflect underlying differences in the derivation of their family systems from an ancestral state. This is because the deep integration of parental care into offspring development that underlies the high dependency of altricial young (see Smiseth *et al.*, 2003; Kölliker, 2007; Badyaev & Uller, 2009) only evolves *after* the emergence of family life (see Section IV.2*a*). Altricial family systems are therefore always derived (and derived systems typically altricial). The relative independence of precocial young, on the other hand, suggests a lower degree of phenotypic integration that more closely resembles an ancestral state (Smiseth *et al.*, 2003; Kölliker, 2007; Falk *et al.*, 2014). Precocial family systems are therefore typically less derived (and non-derived systems always precocial). We are aware that (the similarities between) these dichotomic classifications are coarse, since they actually depict opposing ends of a continuum of developmental modes and evolutionary derivation. Nevertheless, they highlight that precocial [altricial] species can serve as model organisms in the study of non-derived [derived] forms of family life, and we retain these classifications here because their generality makes them useful in our discussion of universal trends shaping the evolution of family life.

III. THE NEGLECTED FACETS OF FAMILY LIFE

Family living is a form of group living. The various fitness effects inherent to all types of group-living – such as the costs of increased competition and the benefits of cooperative foraging – should therefore also be considered in the context of family life (Alexander, 1974; Krause & Ruxton

2002). However, instead of investigating the full range of possible cooperative and competitive family interactions, the last decades of research on family life have predominantly focused on the fitness effects of parental care as well as on the conflicts over (and the cooperation in) its allocation (see Fig. 1; reviewed in Clutton-Brock, 1991; Royle, Smiseth & Kölliker, 2012*a*). This implicit equalization of the fitness effects of parental care with the fitness effects of family life has led to the neglect of three potentially important dimensions of social interactions within the family: (*i*) sibling cooperation, (*ii*) offspring assistance (here defined as cooperative acts of offspring to the benefit of their parents), and (*iii*) parent–offspring competition (an additional poorly explored facet of social life in biparental families, competition between parents, is discussed in Section IV.2*c*). Notable exceptions to this general trend are studies on the highly derived, extended families of cooperative breeders, in which these mechanisms have been explored (but see Section IV.2b). Below, we review examples of the neglected facets of family life. We argue that accounting for the (direct and indirect) fitness effects of these mechanisms is crucial, since they could augment or counteract the benefits and costs of parental care, and thus tip the scales in favour (or in disfavour) of the emergence and subsequent evolution of family life.

(1) Sibling cooperation

Cooperative interactions (i.e. behaviours that provide a benefit to another individual, and are selected for because of this beneficial effect; West, Griffin & Gardner, 2007) are often promoted by kinship, and thus frequently occur among both adult and juvenile siblings (see for, instance, Wilson, 1971; Packer *et al.*, 1991; Krakauer, 2005; Costa, 2006; Sharp, Simeoni & Hatchwell, 2008). In the context of family life, however, only cooperation among adult siblings has been thoroughly explored (see Section IV.2b). By contrast, most studies of social interactions among

juveniles thus far only investigated the conspicuous competitive behaviours of juvenile birds and mammals that compete over access to limited parental resources (reviewed in Mock & Parker, 1997; Roulin & Dreiss, 2012). However, sibling interactions during family life are not competitive by default, and an increasing number of studies report an unexpected diversity of cooperative interactions (and by-product mutualism) among altricial as well as precocial juveniles (reviewed in Roulin & Dreiss, 2012). Indeed, sibling cooperation in family groups is a hallmark of termite societies, where larvae, nymphs, workers and soldiers are all juveniles (Noirot & Pasteels, 1987; Eggleton, 2011). Moreover, it occurs in the house wren *Troglodytes aedon*, where offspring postpone fledging to the benefit of their younger siblings (Bowers, Sakaluk & Thompson, 2013), in the king penguin *Aptenodytes patagonicus*, where huddling improves the juveniles' thermoregulation (Barré, 1984), and in the spotted hyaena *Crocuta crocuta*, where offspring form coalitions with litter mates against unrelated juveniles (Smale *et al.*, 1995). Further examples of sibling cooperation occur in the Mississippi kite *Ictinia mississippiensis* and the ambrosia beetle *Xyleborinus saxesenii*, where offspring express mutual cleaning ('allo-preening'; Botelho, Gennaro & Arrowood, 1993; Biedermann & Taborsky, 2011), in subsocial treehoppers of the tribes Aconophorini and Hoplophorionini, where juveniles exhibit warning colouration ('aposematism'; Lin, 2006), and in many leaf beetles of the subfamilies Cassidinae and Chrysomelinae, where juveniles form defensive rings ('cycloalexy'; Chaboo *et al.*, 2014).

Importantly, juveniles can also cooperate in resource acquisition. In altricial species, such cooperation typically aims at improving the juveniles' access to parental provisioning (see Forbes, 2007). For instance, altricial juveniles sometimes refrain from interfering with their siblings' feeding attempts (e.g. in the blue-footed booby *Sula nebouxii*; Anderson & Ricklefs, 1995) and may even offer parentally provided food items to their siblings (e.g. in the barn owl *Tyto alba;*

Marti, 1989). Moreover, they can coordinate their begging behaviour to increase the parents' feeding rate (e.g. in the in the black-headed gull *Larus ridibundus* and the banded mongoose *Mungos mungo*; Johnstone, 2004; Mathevon & Charrier, 2004; Bell, 2007), or negotiate their share of parental resources to avoid the greater costs of unrestrained sibling rivalry (e.g. in the barn owl *T. alba*, the spotless starling *Sturnus unicolor*, and the meerkat *Suricata suricatta*; Roulin, 2002; Johnstone & Roulin, 2003; Bulmer, Celis & Gil, 2008; Madden *et al.*, 2009; Dreiss *et al.*, 2010). By contrast, cooperation in resource acquisition among precocial juveniles can – at least in principle – occur independently of parental provisioning. For instance, food sharing occurs even without parental involvement in the European earwig *Forficula auricularia* (Falk *et al.*, 2014; Kramer, Thesing & Meunier, 2015) and in many social spiders such as the huntsman spider *Delena cancerides* (Yip & Rayor, 2013, 2014).

In both altricial and precocial species, the fitness effects of sibling cooperation might often be concealed by the effects of parental care. In line with this assumption, it has recently been suggested that larval mass in the burying beetle *Nicrophorus vespilloides* peaks at a higher larval density in the absence of care. This indicates that parental care usually masks the beneficial effect of initial increases in larval density on the brood's ability to penetrate and use the breeding carcass (Schrader *et al.*, 2015*a*). This notwithstanding, the diverse forms and broad taxonomical distribution of cooperative behaviours among juveniles suggest that sibling cooperation in family groups is important during all life stages and might thus play a crucial role during early steps in the evolution of family life (see Section IV).

(2) Parent–offspring competition

Competition between parents and their offspring occurs whenever the utilisation of an essential resource by the parents limits the utilisation of this resource by their offspring – or vice versa. This form of kin competition typically arises with the onset of offspring foraging and/or sexual maturity, and has been predicted to promote offspring dispersal and thus the breakup of family units (Hamilton & May, 1977; Comins, Hamilton & May, 1980; West, Pen & Griffin, 2002; see also Sorato, Griffith & Russell, 2016). This prediction is well supported in altricial species. For instance, parent–offspring competition resulting from experimental food removal hastens the dispersal of male offspring in the altricial western bluebird *Sialia mexicana* (Dickinson & McGowan, 2005), while experimental food supplementation delays offspring dispersal in the cooperatively breeding carrion crow *Corvus corone corone* (Baglione *et al.*, 2006). Furthermore, parent–offspring competition over mating partners ('reproductive competition'; Gaston, 1978; Emlen, 1982*b*; Clutton-Brock, 2017) has been reported in a variety of cooperative breeders ranging from sweat bees (*Halictus ligatus*; Richards, Packert & Seger, 1995) to stripe-backed wrens (*Campylorhynchus nuchalis*; Piper & Slater, 1993) to meerkats (*S. suricatta*; Clutton-Brock *et al.*, 2001). Notably, the costs of this competition can even lead to shifts in offspring sex ratio if parents skew their investment in favour of the sex that disperses (earlier) from the natal site, and thereby minimize the impending competition with their philopatric offspring (Clark, 1978; Silk, 1984; Meunier, West & Chapuisat, 2008; Silk & Brown, 2008). Such an effect of 'local resource competition' has, for instance, been reported in the common brushtail possum *Trichosurus vulpecula*, where mothers compete with their philopatric daughters for dens within the mother's territory (Johnson *et al.*, 2001).

In analogy to its effects in altricial species, parent–offspring competition can also affect offspring dispersal and the duration of family life in precocial species. For instance, parent–offspring competition has been shown to promote offspring dispersal in the solitary common lizard *Lacerta vivipara* (Léna *et al.*, 1998; Le Galliard, Ferrière & Clobert, 2003; Cote, Clobert & Fitze, 2007). Conversely, the prolonged presence of fathers has been shown to reduce offspring survival under food limitation in *N. vespilloides*, a burying beetle with biparental care in which both parents feed on the breeding carcass (Scott & Gladstein, 1993; Boncoraglio & Kilner, 2012). This latter finding suggests that father–offspring competition might partly offset the benefits of paternal care, and thus offers a potential explanation as to why fathers typically leave the brood earlier than mothers in this species. Intriguingly, parent–offspring competition in precocial species might even entirely negate the benefits of family living under certain harsh conditions. In line with this hypothesis, mother–offspring competition under food limitation has been shown to render maternal presence detrimental to the long-term survival of offspring in uniparental families of the European earwig *F. auricularia* (Meunier & Kölliker, 2012; Kramer *et al.*, 2017). Interestingly, highly competitive earwig mothers exhibit both a comparatively bad condition at the beginning of family life, and an increased investment into their next reproductive attempt. The occurrence of mother–offspring competition under food limitation might thus reflect that earwig mothers inadvertently harm their offspring in an attempt to prevent their own starvation and/or to shift their investment from current to future reproduction (Kramer *et al.*, 2017).

In precocial species, the costs of parent-offspring competition are likely often concealed by the benefits of parental care. Indeed, carcasses guarded by *N. vespilloides* fathers are less likely to be taken over by conspecifics, suggesting that the costs of father–offspring competition can be offset by the benefits of offspring defence against infanticide by conspecifics (Scott & Gladstein,

1993). Similar benefits of maternal care might also explain why *F. auricularia* offspring do not disperse earlier under resource limitation (Wong & Kölliker, 2012). Notably, such masking effects of parental care are likely less pronounced in altricial species. This is because parent-offspring competition in these species typically arises towards the end of family life (see the beginning of this section). At this time, the benefits of continuing care are often limited (Bateson, 1994), and thus unlikely to offset the costs of competition entirely. Irrespective of such effects, the multifaceted role of parent–offspring competition in general – and its early onset in precocial species in particular – suggest that it might play a crucial role in the evolution of family life (see Section IV).

(3) Offspring assistance

Cooperation between parents and their offspring is prominently featured in a plethora of studies on parental care (reviewed in Clutton-Brock, 1991; Royle *et al.*, 2012*a*). However, parent–offspring cooperation is not a one-way road and can also involve cooperative behaviours (or by-product mutualism) that offspring direct towards their parents. Such offspring assistance is pervasive in the extended families of cooperative breeders, where adult offspring often assist their parents in raising younger siblings (Wilson, 1971; Bourke & Franks, 1995; Cockburn, 1998; Koenig & Dickinson, 2016). Yet offspring assistance during family life can also be performed by juveniles. Among altricial species, it frequently occurs in eusocial insects where larvae/nymphs can fulfil crucial roles for colony functioning (reviewed in Eggleton, 2011; Schultner, Oettler & Helanterä, 2017). For instance, juveniles can feed the reproductives ('reverse parental care'; Nalepa, 2016) and defend them as soldiers (in virtually all termites; Howard & Thorne, 2011), or take over the extension of galleries and the compressing of waste into compact balls (in the

ambrosia beetle *X. saxesenii*; Biedermann & Taborsky, 2011). Moreover, juveniles can produce silk used in nest construction (in weaver ants of the genus *Oecophylla*; Hölldobler & Wilson, 1977), and act as a 'communal stomach' (Wheeler, 1918; Dussutour & Simpson, 2009) that provisions the queen with secretions necessary for protein degradation (in the metricus paper wasp *Polistes metricus*; Hunt, 1984) or sustained egg production (in pharaoh ant *Monomorium pharaonis*; Børgesen, 1989; Børgesen & Jensen, 1995).

Apart from its role in altricial species with highly complex societal organization, the notion of offspring assistance has received little attention. However, recent findings indicate that parents can also benefit from offspring assistance in precocial species. For instance, parents might benefit from their offspring's investment into shared immune traits (social immunity; (Cremer, Armitage & Schmid-Hempel, 2007; Cotter & Kilner, 2010; Cotter *et al.*, 2010; Meunier, 2015; Van Meyel, Körner & Meunier, 2018), or into independent foraging and defence against predation (Krause & Ruxton, 2002). In line with the former notion, faeces of caring mothers exhibit lower antifungal activity than those of non-caring females in the European earwig *F. auricularia,* suggesting that mothers might downregulate (or at least not compensate for the reduction in) their own investment into nest sanitation during family life, and instead rely on the superior antifungal properties of the faeces of their juveniles (Diehl *et al.*, 2015). Conversely, delayed juvenile dispersal improves the survival of tending mothers in the subsocial spider *Anelosimus studiosus* (Jones & Parker, 2002), a finding that might reflect benefits of offspring investment into prey capture or into the maintenance of the communal web. Indeed, offspring assist in web construction in many social spiders (Yip & Rayor, 2014), suggesting that mothers could regularly benefit by reducing their own investment (such 'load lightening' is well known in cooperative breeders, where helpers can often gain indirect fitness benefits by enabling their parents to produce more siblings; Crick, 1992;

Meade *et al.*, 2010; Johnstone, 2011). Although such benefits of offspring assistance might be concealed by the costs of parental care, they could nevertheless have a significant impact on the evolution of family interactions and, more generally, on the emergence of social life in family units (see Section IV). Overall, it is therefore crucial to investigate the role of offspring assistance and other neglected facets of family life to advance our understanding of the evolution of family life.

IV. THE (EARLY) EVOLUTION OF FAMILY LIFE

The evolution of family life generally presumes that the fitness benefits of family living outweigh the costs of a prolonged association of the family members (Alexander, 1974; Clutton-Brock, 1991; Klug *et al*., 2012). However, the impact of the processes mediating these benefits can change over evolutionary time (Smiseth *et al.*, 2003; Falk *et al.*, 2014; Royle, Alonzo & Moore, 2016). This is because the current benefits associated with a trait (such as a parental behaviour) do not necessarily reflect the adaptive value of this trait in an ancestral state (Williams, 1966; Eberhard, 1975). For instance, the high benefits associated with parental food provisioning in derived family systems typically reflect the dependency of offspring on food provided by the parents, a state that only evolved after the emergence of parental provisioning. The benefits of parental provisioning are thus likely less pronounced in non-derived family systems (Smiseth *et al.*, 2003; Kölliker, 2007; Klug *et al.*, 2012; Royle *et al.*, 2012*b*). Conversely, mechanisms playing a limited role in derived systems might have a more prominent role in less derived systems (Section IV.2*b*). Understanding the evolution of family living therefore requires a 'diachronic' perspective that considers all mechanisms promoting family life and examines their role as they change over time in the evolution of derived from ancestral family systems.

Instead of investigating the full range of mechanisms across different social systems, the last decades of empirical work predominantly followed an incomplete, 'synchronic' approach that largely focused on describing the current benefits and costs of parental care in the derived family systems of altricial vertebrates and eusocial insects (reviewed in Clutton-Brock, 1991; Royle *et al.*, 2012*a*). By contrast, the fitness effects of family interactions in precocial species, which feature facultative forms of family life reminiscent of an ancestral state, have received comparably little attention (but see, for instance, Eggert, Reinking & Müller, 1998; Zink, 2003; Salomon, Schneider & Lubin, 2005; Kölliker, 2007). Similarly, theoretical approaches have thus far only indirectly explored the evolution of family life, since they typically investigated the influence of life-history characteristics, co-evolutionary dynamics, or environmental conditions on the evolutionary origin and maintenance of parental care (Wilson, 1975; Tallamy, 1984; Tallamy & Wood, 1986; Bonsall & Klug, 2011*b*; Klug *et al.*, 2012). As a corollary of this narrow focus on parental care, our current understanding of the early evolution of family life is fragmentary. In the following section, we address this fundamental issue. Specifically, we review the factors promoting the emergence and subsequent evolution of family life, and demonstrate that integrating the costs and benefits of thus far overlooked facets of family living in particular – and the study of precocial family systems in general – entail major changes in our understanding of the evolution of family life.

(1) The emergence of family life

(*a*) *The standard account: the evolution of post-hatching parental care*

The evolutionary emergence of family life has typically been explored indirectly in studies endeavouring to understand which factors favoured the extension of pre-hatching parental care beyond the time of offspring hatching or birth (e.g. Lack, 1968; Clutton-Brock, 1991; Smiseth *et*

al., 2012). These studies suggest that the emergence of parental care – and thus family life – requires the concurrence of factors that jointly make sustained social interactions among family members possible and – should the occasion arise – able to spread in the population (Klug *et al.*, 2012). The initial step in the emergence of family life is promoted by life-history characteristics ensuring that social behaviours are primarily directed towards family members (Tallamy & Wood, 1986; Lion & van Baalen, 2007). This propensity to interact mainly with family members can increase the scope for the evolution of cooperative behaviours (such as parental care and sibling cooperation) by reducing the likelihood that such behaviours are misdirected toward non-kin (Hamilton, 1964; Lion & van Baalen, 2007; but see West *et al.*, 2002). Hence, family life is most likely to emerge if parents and offspring can interact at all (i.e. if parents live long enough and confine their reproduction to specific periods and locations; Tallamy, 1984), and do so frequently due to limited dispersal (Hamilton, 1964; Lion & van Baalen, 2007) and/or kin/familiarity recognition (Evans, 1998; Fellowes, 1998; Dobler & Kölliker, 2011). Additionally, the emergence of family life can be promoted by the presence of precursors of post-hatching care (Tallamy & Wood, 1986; Royle *et al.*, 2012*b*). In line with this idea, the evolution of offspring attendance and guarding has been suggested to derive from ancestral defensive or aggressive behaviours (Tallamy, 1984). Similarly, parental provisioning during family life might have evolved *via* selection acting on – and modifying – self-feeding behaviours (Cunningham *et al.*, 2016), and some effector molecules in social immunity might have been recruited from a function in personal immunity (Palmer *et al.*, 2016).

Once the preconditions for the emergence of family life are met, environmental conditions and effects of (additional) life-history characteristics jointly determine whether it can spread in the population against the background of the prevalent solitary lifestyle (Tallamy, 1984; Tallamy &

Wood, 1986; Clutton-Brock, 1991; Klug *et al.*, 2012). In particular, the evolution of family life is thought to be promoted by four environmental 'prime movers' that variously increase the benefits or decrease the costs of parental care: (*i*) stable and structured habitats; (*ii*) unusually stressful physical environments; (*iii*) high predation pressure; and (*iv*) scarce and specialized food sources (Wilson, 1975; see also Krause & Ruxton, 2002; Botterill-James *et al.*, 2016). Interestingly, these four prime movers might ultimately boil down to differences in the quality as well as the spatial and temporal availability of limited resources, since these attributes will determine how, where, and when animals forage and feed – and what competitors, predators and parasites they will encounter (Tallamy & Wood, 1986). In any case, such environmental conditions typically modify the impact of basic life-history conditions (such as stage-specific mortality and maturation rates) on the benefits and costs of family interactions (Bonsall & Klug, 2011*b*; Klug *et al.*, 2012). For instance, harsh conditions and the concomitant intense competition for limited resources have been predicted to increase the mortality rate of solitary individuals (Wilson, 1975; Clutton-Brock, 1991). This, in turn, should promote the evolution of parental care and thus family life, because the uncertain prospects of future reproduction decrease the relative costs of care to adults (Klug & Bonsall, 2010; Bonsall & Klug, 2011*b*), and increase its potential benefits to offspring (Webb *et al.*, 2002; Klug & Bonsall, 2010). However, empirical findings are sometimes at odds with these predictions. For instance, harsh conditions negate rather than increase the usual benefits of maternal presence and thus family life in the European earwig *F. auricularia* (Meunier & Kölliker, 2012; Kramer *et al.*, 2017). The limited predictive power of the standard account of the evolution of family life (see Costa, 2006; Trumbo, 2012; Capodeanu-Nägler *et al.*, 2016) might partly reflect that environmental conditions, life-history characteristics, and the benefits and costs of parental care often interact in unexpected ways (Bonsall & Klug, 2011*a*,*b*; Meunier & Kölliker, 2012).

However, we believe that it also reflects an excessive focus on a subset of family interactions – and on their expression in a subset of family systems.

(*b*) *An extended account: the role of the neglected facets of family life*

The standard account for the evolutionary origin of family life solely focuses on the extension of parental care beyond offspring emergence, and thus inadvertently neglects the role of other social interactions within the nascent family. However, these neglected facets could have a profound influence on the cost–benefit ratio of family life. In particular, parent–offspring competition (and its potential knock-on effects on sibling rivalry and sexual conflict) could impede the evolution of family life by counteracting the potential benefits of cooperative interactions (such as parental care) among the family members (Meunier & Kölliker, 2012; Kramer *et al.*, 2017). Conversely, both sibling cooperation and offspring assistance could promote the emergence of family life, for example by complementing the (initially limited) benefits of care to offspring, and/or by offsetting some of the costs of family life to parents (see Falk *et al.*, 2014; Kramer *et al.*, 2015). For instance, the benefits of defensive behaviours or food sharing among offspring might complement benefits of parental anti-predator behaviours or parental provisioning, whereas the benefits of offspring aiding their parents in nest/colony maintenance might offset some of the costs of parental care. Intriguingly, these forms of cooperation could themselves evolve from by-product benefits (such as predator dilution effects; Krause & Ruxton, 2002) arising in offspring aggregations.

The benefits of by-product mutualism or sibling cooperation in such offspring aggregations could also affect the initial duration of family life. In particular, they could offer an additional incentive (or even an alternative reason; see Section V.1) for offspring to delay dispersal from their natal site (Kramer *et al.*, 2015), and might thus allow extended periods of family life even before

the emergence of elaborate forms of (post-hatching) parental care. This scenario contrasts with the standard account for the evolution of family life, where the 'simple' extension of parental care beyond offspring emergence (see Michener, 1969; Costa, 2006) should initially only allow for brief periods of family life. This is because the standard account neglects the potential impact of cooperation among offspring, and thus implies that offspring in recently evolved family systems should (still) tend to disperse soon after hatching to avoid the impending competition with their siblings and parents (Hamilton & May, 1977; Comins *et al.*, 1980; West *et al.*, 2002). Longer periods of family living would thus only arise secondarily where the benefits of offspring attendance and other early forms of parental care select for delayed offspring dispersal. From an offspring's point of view, family life is classically thought to evolve *despite* the presence of competing siblings (Hamilton & May, 1977; Comins *et al.*, 1980; West *et al.*, 2002; see also Mock & Parker, 1997; Roulin & Dreiss, 2012). However, the occurrence and potential role of sibling cooperation suggests that family life might rather emerge – or at least be initially favoured – *because of* the presence of siblings.

Similar to the fitness effects of early forms of parental care (see Section IV.1*a*), the impact of other facets of family life likely depends on an intricate interplay of life-history characteristics and environmental conditions. The costs of parent–offspring competition, for instance, will be greatest if parents and offspring feed on the same resources, and simultaneously forage in the same area (but could be reduced where parents and/or offspring increase their foraging range or diversify their diet; see also Kramer *et al.*, 2017). Moreover, the costs of parent–offspring competition might increase if parents overproduce offspring (for instance as an insurance against the unexpected early failure of some of the juveniles; Forbes, 1991). The benefits of cooperative interactions among offspring, on the other hand, might be greatest if they can function as a buffer against

environmental variability, or if they allow for synergistic effects. For instance, reciprocal food sharing (such as in the vampire bat *Desmodus rotundus*; Wilkinson, 1984; Carter & Wilkinson, 2013) might help offspring to buffer against variability in parental provisioning rates (Kramer *et al.*, 2015) or variation in the local availability of resources (and thus in foraging success; Rubenstein, 2011; Koenig & Walters, 2015). Conversely, synergistic effects of sibling cooperation might allow offspring to overcome the chemical defences of host plants (Dussourd & Denno, 1991), break through plant material (Ghent, 1960) or amplify the deterrent effect of offspring warning colouration (Ruxton, Sherratt & Speed, 2004). Finally, the possible spectrum of different types of sibling cooperation and offspring assistance is likely subject to developmental constraints (see Maynard Smith *et al.*, 1985), where certain types of behaviours cannot be performed effectively by immatures.

Besides these life-history traits, the environmentally determined spatiotemporal availability and quality of resources are likely crucial factors shaping the fitness effects of the neglected facets of family life (in addition to their effect on the fitness effects of parental care; see Section IV.1*a*). For instance, abundant and persistent resources (including plant materials such as foliage and wood) should generally limit the scope for intra-familial competition, and could select for sibling cooperation in foraging or anti-predator defence (e.g. Lin, 2006; Chaboo *et al.*, 2014) and offspring assistance in nest or colony maintenance (e.g. Howard & Thorne, 2011; Biedermann & Taborsky, 2011) because they are often poorly digestible and exposed to predation (Tallamy & Wood, 1986). Widely dispersed 'bonanza' resources (such as carrion or dung), by contrast, could variously promote both intra-familial competition *and* cooperation. On the one hand, these 'ephemeral' resources typically decay quickly and should thus select for forms of sibling cooperation (and parental care; Wilson, 1975; Tallamy & Wood, 1986) that promote rapid

offspring development (Schrader *et al.*, 2015*a*). On the other hand, these resources are ultimately finite and hard to find, and could thus promote (parent–offspring) competition (Scott & Gladstein, 1993; Keppner, Ayasse & Steiger, 2018). A similar tug-of-war between cooperation and competition might also accompany the use of other dispersed resources such as prey and organic detritus (including seeds, fruit, and fallen leaves). In particular, the spatiotemporal dispersion of these resources could favour sibling cooperation in prey capture or the sharing of independently acquired food (e.g. Yip & Rayor, 2014; Falk *et al.*, 2014; Kramer *et al.*, 2015), and might promote offspring assistance in social immunity (e.g. Reavey, Beare & Cotter, 2014; Diehl *et al.*, 2015) where earlier selection for parental care has promoted family living in underground nests or burrows (Tallamy & Wood, 1986). However, a wide dispersion and/or poor quality of resource patches or prey could also promote parent–offspring competition (e.g. Meunier & Kölliker, 2012; Kramer *et al.*, 2017).

Notably, the often contrasting effects of environmental conditions on the different facets of family life illustrate that all types of family interaction jointly determine whether or not family life evolves. For instance, environmental harshness and the accompanying limitation of crucial resources has been predicted to promote the evolution of parental care (Wilson, 1975; Clutton-Brock, 1991). However, resource limitation also increases the scope for parent–offspring competition and sibling rivalry, which in turn decreases the propensity of juveniles to cooperate with their siblings or parents (West *et al.*, 2002; Frank, 2003; see also Section IV.2*b*). Some harsh conditions might thus select against the evolution of family life despite the expected high benefits of parental care (Webb *et al.*, 2002; Klug & Bonsall, 2010). Overall, such as yet poorly explored effects might help to explain why even closely related species exposed to ostensibly identical

conditions often differ in the occurrence and nature of family interactions (see Costa, 2006; Trumbo, 2012; Capodeanu-Nägler *et al.*, 2016).

(2) The consolidation of family life

(*a*) *The standard account: the evolution of elaborate care*

After the emergence of family units, co-evolutionary feedback loops between parental and offspring traits are expected to promote the evolution and diversification of parental care, and thus to lead to the rapid consolidation of family life (Wolf, Brodie & Moore, 1999; Kölliker, Royle & Smiseth, 2012; Uller, 2012; Jarrett *et al.*, 2017). For instance, the initial evolution of parental provisioning may trigger evolutionary changes in other components of care as well as in offspring traits, allowing parents to choose safer nest sites, but also increasing the competition among offspring for parentally provided food. This increased sibling rivalry may, in turn, further advance the evolution of parental provisioning, thereby closing the co-evolutionary feedback loop between parental provisioning, the choice of safer nest sites, and sibling rivalry (Smiseth, Lennox & Moore, 2007; Gardner & Smiseth, 2011). Such mutual reinforcement between parental and offspring traits has been predicted to promote a unidirectional trend from simple (ancestral) toward complex forms of family life by fostering an increasingly tight phenotypic integration of parental care and offspring development (Wilson, 1975; Gardner & Smiseth, 2011; Kölliker *et al.*, 2012; Uller, 2012; Royle *et al.*, 2016). In addition to promoting high levels of sibling rivalry, this phenotypic integration often results in an increasing control of parents (and a decreasing control of offspring) over resource allocation, and thus leads to high levels of parent–offspring conflict over the amount of parental investment (Trivers, 1972, 1974), which in turn promote the evolution of offspring behaviors aimed at manipulating their parents into providing more care (see Figure 1; Trivers,

1974; Royle, Hartley & Parker, 2002). In the highly derived family systems of altricial species, the phenotypic integration of parental care into offspring development is advanced to such an extent that juveniles cannot survive without at least some care early in their life (Kölliker, 2007; Uller, 2012).

(*b*) *An extended account I: the (changing) role of the neglected facets of family life*

The increasingly tight phenotypic integration of parental care evolving during the consolidation of family life could have a profound effect on the relative importance of the neglected facets of family life. For instance, the evolution of parental provisioning and the concomitant increased reliance of offspring on parentally provided food likely leads to a delayed onset of offspring foraging (*cf*. Gardner & Smiseth, 2011), and should thus reduce the scope for competition between parents and their offspring. As a result, the impact of parent–offspring competition on family dynamics might steadily decline over the course of the consolidation of family life (Kramer *et al.*, 2017). Similarly, siblings might be most likely to cooperate with each other as long as they are (still) largely independent of parental care. This is because an increased dependency on care is typically paralleled by increased sibling rivalry (Gardner & Smiseth, 2011), and should thus decrease the levels of sibling cooperation (Frank, 1998, 2003). Finally, an increased offspring dependency is likely also accompanied by greater developmental constraints (see Maynard Smith *et al.*, 1985) on the type of social behaviours that the immature juveniles can perform, suggesting that both sibling cooperation and offspring assistance might occur less frequently in altricial than in precocial species. Overall, these considerations indicate that parent–offspring competition, sibling cooperation, and offspring assistance might fulfil crucial roles in ancestral family systems, but

could lose ground where the consolidation of family life promotes an increasingly tight phenotypic integration of parental care into offspring development.

While the role of parent–offspring competition, sibling cooperation, and offspring assistance in nuclear families thus far has received little attention, their impact on the evolution of the extended families of cooperative breeders has been explored more thoroughly (e.g. Bourke & Franks, 1995; Baglione *et al.*, 2006; Koenig & Dickinson, 2016; Sorato *et al.*, 2016). Interestingly, all three facets play a prominent role in shaping these systems: parent–offspring competition can impede the evolution of cooperative breeding (Baglione *et al.*, 2006; Sorato *et al.*, 2016), siblings within breeding groups frequently cooperate with each other (e.g. during group foraging or in defence against predation), and offspring assistance in the form of alloparental care (often called 'help') is the very foundation of cooperative breeding (Skutch, 1935; Cockburn, 1998; Koenig & Dickinson, 2016). However, while these mechanisms usually involve juveniles in nuclear families (which normally dissolve once offspring reach maturity; Clutton-Brock, 1991), they typically involve adult offspring in the extended families of cooperative breeders (where the high dependency on [allo-]parental care limits the scope for these mechanisms in juveniles; see the beginning of this section). Notably, the resurgence of these mechanisms in cooperative breeders after their demise during the consolidation of (nuclear) family life is in line with a key role of offspring dependency in determining their occurrence. Like juveniles in ancestral family systems, adult offspring in cooperative breeders are largely independent of parental care, a situation that increases the scope for parent–offspring competition, but also allows offspring to avoid the impending local competition with their siblings, and thus prevents the high levels of sibling rivalry that usually reduce the likelihood that sibling cooperation and offspring assistance occur.

Notably, this putatively similar role of the neglected facets in ancestral and cooperatively breeding families suggests that the extensive literature on the evolution of cooperative breeding (reviewed in Brown, 1987; Koenig & Dickinson, 2004, 2016; Solomon & French, 2007) could serve as a valuable guideline for studies on the evolution of family life. In particular, the evolution of cooperatively breeding families has traditionally been described as a two-step process that might – in a similar form – also occur during the emergence of (nuclear) family groups. During this process, an individual must first decide whether or not to delay dispersal and remain in its natal group. In the second step, the individual must then decide whether or not to cooperate with its family members (Emlen, 1982*a*; Brown, 1987; Ligon, 1991). In cooperative breeders, the first step is usually attributed to ecological conditions or life-history characteristics that reduce the benefits of dispersal (e.g. by constraining independent breeding) and/or increase the benefits of philopatry (e.g. by increasing survivorship; see Cockburn, 1998; Hatchwell & Komdeur, 2000; Hatchwell, 2009; Komdeur *et al.*, 2017 for reviews). The second step then depends on the (direct and indirect) benefits *versus* costs of assisting parents in raising younger siblings (Cockburn, 1998; Heinsohn & Legge, 1999; Griffin & West, 2003).

Envisioning the evolutionary emergence of (nuclear) family life as such a two-step process immediately prompts two inferences. First, it suggests that the initial formation of family units is not necessarily driven by the benefits of parental care. Instead, offspring might initially delay dispersal to reap the benefits of by-product mutualism in juvenile aggregations (see Section V.1). Similarly, parents might initially associate with their offspring because they derive direct benefits from this association. In this scenario, parental care [sibling cooperation] could arise secondarily if selfish (e.g. defensive) behaviours of parents [offspring] provide by-product benefits to nearby offspring (see also Section IV.1*a*). Second, envisioning the emergence of family life as a two-step

process suggests that an explicit consideration of both the fitness effects of philopatry and dispersal is crucial to understand the conditions favouring the initial formation of family units. For instance, high predation pressure presumably favours family life not only because it increases the potential benefits of cooperative interactions such as parental care and sibling cooperation (see the beginning of this section), but also because it increases the costs of dispersal for offspring (see also Queller & Strassmann, 1998). Across-species variation in the net fitness effects of dispersal *versus* philopatry might also explain why resource limitation and the resulting local competition among family members favours dispersal in some situations (e.g. in the termite *Cryptotermes secundus*; Korb & Schmidinger, 2004) and philopatry in others (e.g. in the European earwig *F. auricularia*; Wong & Kölliker, 2012; Kramer *et al.*, 2017). Finally, note that further possibilities to apply advanced frameworks for cooperative breeding to the emergence of family life could, for instance, relate to the potential impact of additional environmental characteristics (such as variability and harshness; Jetz & Rubenstein, 2011; Koenig & Walters, 2015; Cornwallis *et al.*, 2017) and life-history traits (such as longevity; Downing, Cornwallis & Griffin, 2015).

(*c*) *An extended account II: the rocky road to complex family systems*

Despite the expected trend towards complex family systems (Wilson, 1975; Gardner & Smiseth, 2011; Kölliker *et al.*, 2012; Uller, 2012; Royle *et al.*, 2016), simple family life still abounds across taxa (e.g. Tallamy & Schaefer, 1997; Lin, Danforth & Wood, 2004; Filippi *et al.*, 2009). This indicates that some as yet unknown factors counteract the consolidation of family life and thus prevent an increase in social complexity. For instance, the consolidation of family life might be selected against if the benefits of increased parental care are entirely offset by a decrease in the benefits of sibling cooperation or offspring assistance resulting from the increased offspring

dependency that typically parallels increases in parental care (see Section IV.2*b*). This could be the case in folivorous insects, where the potential benefits of parental care beyond defence against predation are limited due to the high availability of food for the offspring (Costa, 2006) – and where an increased offspring dependency following the evolution of additional forms of care might compromise the ability of juveniles to show cooperative defences themselves. Alternatively or additionally, high parental mortality during family life could counteract its consolidation. Long-term and transgenerational costs of parental loss (such as impaired development of juveniles) are not restricted to altricial family systems (e.g. Harlow & Suomi, 1971; Gonzalez *et al.*, 2001; Fleming *et al.*, 2002; Andres *et al.*, 2013), but can also occur in more ancestral precocial species (Thesing *et al.*, 2015). This finding suggests that even though precocial juveniles can often survive the early death of their parents, they will still suffer (non-lethal) consequences of parental loss. Accordingly, high parental mortality rates might not only increase the likelihood that these negative consequences arise; rather, they might also select against the further consolidation of family life, since the concomitant deepened integration of parental care into offspring development would increase the costs of parental loss. Similarly, the consolidation of family life might be hindered where (variation in) the availability of limited resources prevents parents from reliably provisioning their offspring. Such situations could select against offspring relinquishing control over resource acquisition, and instead promote the maintenance of alternative survival strategies among juveniles (Kölliker, 2007; Kramer *et al.*, 2015; Kramer & Meunier, 2016*b*; Jarrett *et al.*, 2017; Schrader *et al.*, 2017). We surmise that the reliability of parental care – i.e. the likelihood that offspring indeed receive care once it has originated – will prove crucial in determining whether a given family system evolves towards increasing complexity.

Advanced family systems are typically caught in a parental trap that enforces the maintenance of family life irrespective of its current adaptive value (Eberhard, 1975). By contrast, less-derived forms of family life can be lost over evolutionary time (Tallamy & Schaefer, 1997; Lin *et al.*, 2004; Filippi *et al.*, 2009). In the light of the above considerations, this contrast indicates the existence of a threshold of social complexity that determines whether family life is self-sustaining. Above this threshold, the phenotypic integration of parental care into offspring development would be tight enough to render at least one parental care trait obligatory for offspring survival (for instance, nest construction in the phyllode-gluing thrip *Dunatothrips aneurae* is essential, whereas nest hygiene (still) appears to be facultative; Gilbert & Simpson, 2013; Gilbert, 2014). Family life would then be beneficial to offspring irrespective of the external conditions and could thus hardly ever be lost. By contrast, the integration of parental care into offspring development below this threshold would be sufficiently limited to enable offspring survival in the absence of the parents. In this situation, family life would remain facultative, and the interplay between environmental conditions, life-history characteristics and the cost–benefit ratio of all types of family interactions would determine whether family life is maintained at its *status quo*, abandoned in favour of a solitary lifestyle, or propelled towards the threshold that separates facultative from obligatory family systems. The existence of a similar threshold (or point of no return) has been invoked to explain the transition from facultative to obligatory eusociality (Wilson & Hölldobler, 2005). With regard to the evolution of family life, such a threshold would reconcile the current debate over the loss of parental care and family life (see Trumbo, 2012), since it allows for the co-existence of stable as well as unstable family systems. It would also leave scope for the theoretically expected unidirectional trend toward increasingly complex family systems – namely if the prevailing conditions are favourable and stable enough to promote an ever-increasing

integration of parental and offspring traits. Animal groups such as burying beetles of the genus *Nicrophorus* or cockroaches of the subfamily Panesthiinae that feature both species with facultative and species with obligatory family life could be prime models to study these possibilities (see Capodeanu-Nägler *et al.*, 2016).

During the consolidation of family life, parents of the previously non-caring sex sometimes join their family and start providing care on their own. Biparental family systems resulting from this process are rare in invertebrates, fishes and mammals, but occur more commonly in amphibians and predominate among birds [see Balshine (2012) and Trumbo (2012) and references therein]. Across taxa, the evolution of biparental families is typically favoured where males can derive greater benefits by joining rather than abandoning their offspring and the caring female – a situation that can, for instance, arise if future reproductive opportunities are limited and/or if the combined effort of two parents is necessary to construct or defend a valuable resource used for breeding (e.g. Gonzalez-Voyer, Fitzpatrick & Kolm, 2008; Remeš *et al.*, 2015; Gilbert & Manica, 2015). Due to its impact on sexual conflict and the evolution of mechanisms for its resolution, the social life in biparental families has received close theoretical and empirical scrutiny over the last decades (reviewed in Kokko & Jennions, 2012; Lessells, 2012; Royle *et al.*, 2016; Smiseth & Royle, 2018). Yet it has largely escaped notice that the evolution of biparental families also introduces scope for a fourth neglected facet of family life: competition between parents. Such competition, for instance, likely occurs in the biparental burying beetle *N. vespilloides*. In this species, both parents feed on the carcass deployed for breeding (Scott & Gladstein, 1993; Boncoraglio & Kilner, 2012), and it has recently been shown that an increased carcass consumption of food-deprived males exacerbates the weight loss of their partner during the period of active care (Keppner *et al.*, 2018). Intriguingly, females seem to match an increased

consumption by their partner by increasing their own weight gain, suggesting the existence of mechanisms mediating the resolution of this conflict over carcass consumption (Pilakouta, Richardson & Smiseth, 2016). This notwithstanding, competition between parents introduces an additional cost to family life, and thus likely counteracts the evolution of (biparental) families.

V. IMPLICATIONS FOR SOCIAL EVOLUTION

Throughout the history of life on earth, previously independent units (such as cells) have formed social collectives (such as multicellular organisms) to cope with the challenges imposed by their changing environment. Transitions from solitary to social life were the incipient steps in such major transitions in evolution, and hence often had far-reaching repercussions on the diversity, complexity, and hierarchical organization of life itself (Maynard Smith & Szathmáry, 1995; Bourke, 2011). Indeed, the quest for general mechanisms driving such transitions has taxed scientists ever since Darwin (1859) first speculated on the evolution of eusocial societies (see Alexander, 1974; Krause & Ruxton, 2002; Bourke, 2011). Since then, the mechanisms driving transitions from simpler social systems to the highly integrated and often permanent societies of cooperatively breeding vertebrates and eusocial insects have been thoroughly explored (e.g. Wilson, 1971; Bourke & Franks, 1995; Crozier & Pamilo, 1996; Koenig & Dickinson, 2004, 2016). The evolutionary origin of the simpler social systems themselves, however, has received less attention (Trumbo, 2012; Falk *et al.*, 2014; van Gestel & Tarnita, 2017; Boomsma & Gawne, 2018), and the mechanisms promoting the early evolution of social life remain poorly understood. The emergence of family living exemplifies a transition from solitary to social life, and marks the origin of an (initially) simple social system. Moreover, it constitutes the initial step towards the major transition to eusociality (Maynard Smith & Szathmáry, 1995; Bourke, 2011; Boomsma &

Gawne, 2018). Understanding the origin and consolidation of family life might thus help to shed light on processes that also shape (the early steps of) other evolutionary transitions (see also van Gestel & Tarnita, 2017). Below, we discuss how adopting a broad perspective on the evolution of family life could provide general insights into the factors shaping social evolution.

(1) Pathways to group formation

Social interactions among juveniles likely have a crucial impact on the early evolution of family units (see Section IV.1*b*); yet their impact could go beyond the simple augmentation of the benefits of parental care. In particular, the benefits of such interactions might influence the initial formation of family units, and could thus have general implications for our understanding of the transitions to group living. Family living is typically envisioned to evolve following the subsocial pathway, where group formation results from parents staying with and caring for their offspring (Wilson, 1971; Clutton-Brock, 1991; Queller, 2000). However, simple social groups can also arise as the consequence of gregarious behaviour of related and/or unrelated individuals of the same generation. For instance, such gregarious behaviour gave rise to the larval societies found among many sawflies, grasshoppers, caterpillars and chrysomelids (Costa, 2006). Notably, the potential role of sibling cooperation during early stages of the evolution of family life suggests that such aggregations of juveniles might not only constitute an alternative pathway to group formation; rather, they could actually precede the emergence of (subsocial) family life. Specifically, aggregations of juveniles could initially arise whenever the (by-product) benefits of sibling interactions favour delayed dispersal, and might subsequently give rise to families if parents extend already existing forms of pre-hatching care beyond offspring emergence (e.g. Lack, 1968; Clutton-Brock, 1991; Smiseth *et al.*, 2012). The finding that larval gregariousness preceded family-living

in leaf beetles of the subfamily Cassidinae is in line with this idea (Chaboo *et al.*, 2014). A species might thus not only exhibit both the subsocial and the 'gregarious' pathway to group formation during different stages of its life cycle (Costa, 2006); rather, it might follow the two pathways at different times in the course of its evolutionary history.

Apart from their relevance for the initial formation of family groups, social behaviours of juveniles might also be relevant in explaining the evolution of extended family groups featuring alloparental care. In eusocial insects, such families are often classified into 'life insurers' and 'fortress defenders'. According to this classification, life insurers (ants, bees, and wasps) mainly cooperate to ensure offspring survival, whereas fortress defenders (termites, thrips, and aphids) first and foremost cooperate to defend a valuable resource that provides both food and shelter (Queller & Strassmann, 1998; Strassmann & Queller, 2007). Notably, life insurers generally evolved from parental ancestors featuring highly altricial young (Queller & Strassmann, 1998). Given that a high offspring dependency likely limits the scope for offspring cooperation (see Section IV.2*b*), this indicates that sibling cooperation and offspring assistance by juveniles contributed little to the emergence of the extended families of life insurers (cooperation by adult offspring is a hallmark of all eusocial societies). The ancestors of fortress defenders, on the other hand, were not necessarily parental, and typically feature less-helpless young (Queller & Strassmann, 1998; Costa, 2006; but see Nalepa *et al.*, 2008). Sibling cooperation and offspring assistance by juveniles should hence have played a greater role in the evolution of fortress defenders. Indeed, the soldier morph, the first specialized caste to evolve in fortress defenders (Costa, 2006), typically consist of juveniles in aphids and termites (Stern & Foster, 1996; Eggleton, 2011). This suggests that a consideration of the neglected facets of family life could also improve our understanding of both the formation and transformation of family groups.

(2) The rise and fall of cooperation and conflict

In the course of major evolutionary transitions, cooperation typically spreads among lower-level units (such as individuals in the transition to eusociality) and replaces the initially prevailing conflicts between them (Bourke, 2011). The evolution of family life shows evidence for both processes: parental care, a hallmark cooperative trait (Hamilton, 1964; Smiseth *et al.*, 2012), greatly diversifies during the evolution of complex family systems. Conversely, the initially prevailing direct competition between parents and offspring might be progressively suppressed (Kramer *et al.*, 2017). However, the evolutionary dynamics shaping family living also indicate that not all forms of cooperation might be favoured and not all conflicts equally suppressed during its consolidation. For instance, cooperation among juvenile siblings might occur frequently in facultative family systems, but is arguably rare in advanced systems with obligatory family life (Roulin & Dreiss, 2012; Kramer *et al.*, 2015). Conversely, sibling rivalry and parent–offspring conflict (*sensu* Trivers, 1974) typically increase during the evolution of complex family systems (Gardner & Smiseth, 2011). Unsurprisingly, this increase in turn prompts the evolution of specific and often highly elaborate mechanisms of conflict resolution (reviewed in Parker *et al.*, 2002; Ratnieks, Foster & Wenseleers, 2006; Royle *et al.*, 2016; Smiseth & Royle, 2018). Overall, these findings suggest that some conflicts that are characteristic of later stages in an evolutionary transition might arise from dynamics that shaped earlier stages of that transition. In more general terms, they indicate that the increase in cooperation and the suppression of conflicts might be overall trends that need to hold true neither for all types of cooperation and conflict, nor for all stages of a transition. Notably, social systems might evolve towards a major transition even if a specific form of cooperation [such as sibling cooperation] is lost – namely if its benefits are offset

by the benefits of a simultaneous increase in another form of cooperation [such as parental care] and/or the reduction in the costs of some form of conflict [such as parent–offspring conflict].

(3) The consolidation of social life

The various stages of a major transition broadly fall into two categories describing the initial formation of collectives (such as groups) out of formerly independent particles (such as individuals) on the one hand, and the subsequent transformation of these collectives on the other hand (Bourke, 2011). This transformational phase entails the transfer of key (e.g. metabolic or reproductive) functions from the particle to the collective level (Maynard Smith & Szathmáry, 1995; Bourke, 2011), and hence exhibits a striking resemblance to the consolidation of family life. In both cases, an increasingly tight phenotypic integration ties the fate of single particles [offspring] closer and closer to the fate of the collective [family], eventually resulting in obligatory social life – that is the inability of particles [offspring] to survive alone. This resemblance suggests that the reliability with which particles can derive benefits from the collective might have a crucial role in the transformational phase that corresponds to the role of the reliability of parental care in the consolidation of family life (see Section IV.2*c*). For instance, the likelihood of a costly collapse of a facultative collective (i.e. the likelihood of 'collective mortality') might influence whether the phenotypic integration among its constituent particles proceeds, and could thus ultimately determine whether the collective becomes obligatory for particle survival. Like the shift from facultative to obligatory family life, the shift from facultative to obligatory collectives could occur when environmental conditions and life-history characteristics of the particles allow for the breaching of a threshold of social complexity (see Section IV.2*c*). Interestingly, the increasing phenotypic integration among the particles underlying this shift might also be paralleled by a shift

from particle- to collective-level selection (Okasha, 2005; Shelton & Michod, 2010). This change in the most relevant level of selection could in turn determine whether kin-selection or multilevel-selection approaches best describe the underlying evolutionary process (Kramer & Meunier, 2016*a*; Okasha, 2016). The different stages of the evolution of family life offer rich opportunities to investigate these possibilities. Exploring the intricacies of family life might thus be a good starting point to advance our understanding of the major evolutionary transitions and the theoretical framework of sociobiology.

VI. CONCLUSIONS

(1) Over the last decades, the intricacies of family interactions received theoretical and empirical scrutiny in a plethora of studies that focused on parental care and its associated family interactions (such as those arising from sibling rivalry and parent–offspring conflict), and investigated these phenomena in altricial vertebrates and eusocial insects. This historical bias bears on the often-substantial fitness effects of these phenomena in derived family systems. However, it has led to a neglect of mechanisms that might be particularly important in shaping social life in less-derived family systems. Consequently, a coherent framework for the study of social interactions and fitness effects of family life is currently missing, and our understanding of the (early) evolution of family life remains limited.

(2) Here, we argue that the explicit consideration of thus-far neglected facets of family life – and their study across the whole taxonomic diversity of family systems – is crucial to shed light on the mechanisms driving the evolution of social life in family groups. In particular, we illustrate that the strong focus on parental care in advanced social systems has fostered the neglect of three facets of family life: sibling cooperation, parent–offspring competition, and offspring assistance. We

suggest that the impact of these facets is often – and especially in derived family systems – concealed by the fitness effects of parental care.

(3) We show how accounting for these overlooked facets – and their changing role in the course of evolution – is nevertheless crucial, and improves our understanding of the evolutionary emergence and consolidation of family life. Specifically, we highlight that both sibling cooperation and offspring assistance could promote the evolutionary emergence of family life by, respectively, complementing the benefits and offsetting some of the costs of parental care. Conversely, we suggest that parent–offspring competition might impede the evolution of family life by counteracting the benefits of care. We argue that all three thus-far neglected facets have a greater impact where offspring are largely independent of (and thus do not compete for) parental care – a scenario that prevailed during the early evolution of family life, and is prevalent among contemporary precocial species and in adult offspring of cooperative breeders.

(4) We show that the study of family interactions in (precocial) species featuring non-derived forms of family life is not restricted to elucidating the role of sibling cooperation, parent–offspring competition, and offspring assistance; rather it can also shed light on factors – such as the reliability of the benefits of parental care – that can affect the benefits of a (further) consolidation of family life, and thus promote or hamper the evolution of complex animal societies.

(5) Finally, we discuss how a 'diachronic' perspective on the evolution of family living could provide novel insights into the mechanisms driving social evolution. In particular, we suggest that (subsocial) family life can evolve secondarily from aggregations of juveniles that delay dispersal to reap the benefits of sibling cooperation. We argue that the role of the reliability of the benefits of parental care in the consolidation of family life can be generalized, which would suggest a key role of the reliability of 'collective' benefits in the consolidation of social life.

(6) Overall, we aim at providing a general perspective on the evolution of family life that accounts for all types of family interaction across the whole taxonomical diversity of family systems. Recent advances in the study of parental care stress its multifaceted nature (e.g. Gardner & Smiseth, 2011; Royle *et al.*, 2016; Andrews, Kruuk & Smiseth, 2017); we hope that our perspective on the intricacies of family life complements this fruitful trend by raising awareness of the multifaceted nature of social life in family groups. The further development of this perspective hinges on studies that investigate family life in species with non-derived (facultative) forms of family life. Many allegedly 'primitively social' insects [see Tallamy & Wood (1986), Costa (2006), Trumbo (2012) and Wong *et al.* (2013) for reviews] offer unprecedented opportunities to study the origin and maintenance of early forms of parental care and family life (Smiseth *et al.*, 2003; Kölliker, 2007; Trumbo, 2012). We believe that their resemblance to ancestral family systems, and the great diversity of family interactions across species, could well render them prime models of social evolution.

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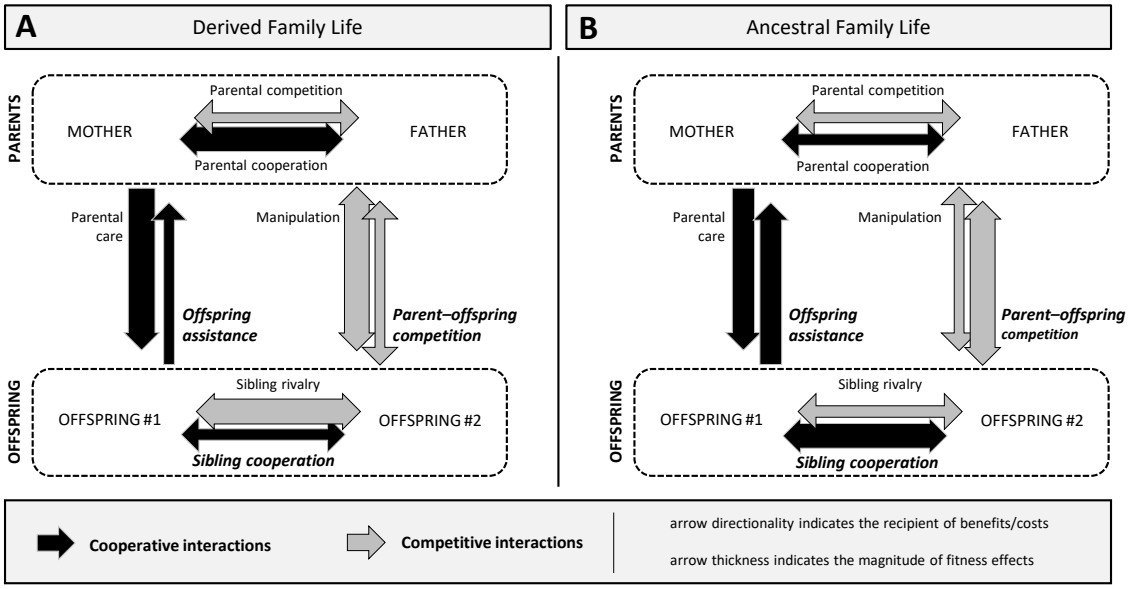

Fig. 1. Social interactions during family life. Cooperative and competitive interactions (represented, respectively, by black and grey arrows) that can potentially occur among family members in (A) derived and (B) ancestral family systems. Research on family interactions has traditionally focused on altricial vertebrates and eusocial insects, and typically investigated the expression and fitness effects of parental care and the conflicts over (and cooperation in) its allocation. While this strong focus is understandable in the light of the often substantial fitness effects of these phenomena (indicated by the thickness of the corresponding arrows) in derived family systems, it has inadvertently fostered the neglect of other facets of family life (in bold italic print). However, these neglected facets might have played a crucial role in shaping ancestral forms of family life. Notably, the social dynamics in ancestral family systems might be very similar to the dynamics in the extended families of many cooperative breeders.