

# 1 **The evolution of social life in family groups**

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## 10 **ABSTRACT**

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

29 **Keywords:** family life; parental care; group-living; evolutionary transition; social evolution;  
30 sociality; precocial; altricial; parent-offspring conflict; sibling rivalry

31	<b>CONTENT</b>	
32	<b>I. INTRODUCTION</b>	<b>4</b>
33	<b>II. THE SEMANTICS OF FAMILY LIFE</b>	<b>7</b>
34	<b>III. THE NEGLECTED FACETS OF FAMILY LIFE</b>	<b>11</b>
35	<b>(1) SIBLING COOPERATION</b>	12
36	<b>(2) PARENT-OFFSPRING COMPETITION</b>	13
37	<b>(3) OFFSPRING ASSISTANCE</b>	15
38	<b>III. THE (EARLY) EVOLUTION OF FAMILY LIFE</b>	<b>17</b>
39	<b>(1) THE EMERGENCE OF FAMILY LIFE</b>	19
40	<i>(a) The standard account: the evolution of post-hatching parental care</i>	19
41	<i>(b) An extended account: the role of the neglected facets of family life</i>	21
42	<b>(2) THE CONSOLIDATION OF FAMILY LIFE</b>	23
43	<i>(a) The standard account: the evolution of elaborate care</i>	23
44	<i>(b) An extended account I: the (changing) role of the neglected facets of family life</i>	24
45	<i>(c) An extended account II: the rocky road to complex family systems</i>	26
46	<b>IV. IMPLICATIONS FOR SOCIAL EVOLUTION</b>	<b>28</b>
47	<b>(1) PATHWAYS TO GROUP FORMATION</b>	29
48	<b>(2) THE RISE AND FALL OF COOPERATION AND CONFLICT</b>	30
49	<b>(3) THE CONSOLIDATION OF SOCIAL LIFE</b>	32
50	<b>VI. CONCLUSIONS</b>	<b>33</b>
51	<b>VII. ACKNOWLEDGEMENTS</b>	<b>35</b>
52		

## 53 I. INTRODUCTION

54 Social life in family groups is a highly variable phenomenon that occurs widespread across the  
55 animal kingdom. Family groups can not only be found in vertebrates such as mammals, birds and  
56 (non-avian) reptiles, but also in numerous invertebrates including arthropods, molluscs and  
57 annelids (Clutton-Brock, 1991; Trumbo, 2012; Wong, Meunier, & Kölliker, 2013). Both within  
58 and across these taxa, families can vary tremendously in terms of composition, persistence and  
59 intimacy of social interactions (Klug, Alonso, & Bonsall, 2012; Trumbo, 2012). For instance,  
60 family groups can be composed of offspring and either their mother, their father, or both parents;  
61 they can last from only few hours to an entire lifetime; and they can range from temporary and  
62 facultative aggregations over cooperatively breeding groups to highly integrated eusocial  
63 societies featuring reproductive division of labour (Hölldobler & Wilson, 1990; Costa, 2006;  
64 Koenig & Dickinson, 2016).

65 The emergence of family life is commonly thought to constitute a transition from solitary  
66 to social life, and marks the initial step in the *major evolutionary transition* to eusociality  
67 (Maynard Smith & Szathmáry, 1995; Bourke, 2011). This is because the origin of family life  
68 entails the emergence of a novel – social – environment (cf. Badyaev & Uller, 2009; Uller, 2012)  
69 that can not only become an integral part of an organism's life-history (Clutton-Brock, 1991;  
70 Gross & Clutton-Brock, 2005; Wong *et al.*, 2013), but may also create long-lasting bonds  
71 between parents and their offspring. Such bonds preceded the evolution of many derived social  
72 behaviours (Darwin, 1871; Wilson, 1975; Royle, Smiseth, & Kölliker, 2012a), and thus likely  
73 drove the transformation of simple family systems to advanced animal societies. Eusocial  
74 societies, for instance, likely arose from family units in which offspring delayed dispersal and

75 independent reproduction, and instead assisted their parents in raising younger siblings  
76 (Boomsma & Gawne, 2017). Studying family life can thus help elucidating factors that shape the  
77 evolution of complex animal societies (e.g. Wheeler, 1928; Michener, 1969; Wilson, 1975;  
78 Bourke, 2011), and more generally shed light on mechanisms that commonly promote the  
79 emergence and maintenance of social life in nature.

80         Despite its crucial role in social evolution, the origin and maintenance of family life is  
81 somewhat surprisingly often only touched upon indirectly in studies focusing on parental care  
82 (but see, for instance, (Falk *et al.*, 2014; Jarrett *et al.*, 2017). Parental care comprises a variety  
83 of traits ranging from gamete provisioning over nest construction to brood attendance and food  
84 provisioning (reviewed in Clutton-Brock, 1991; Costa, 2006; Smiseth, Kölliker, & Royle, 2012;  
85 Wong *et al.*, 2013), and generally encompasses “any parental trait that enhances the fitness of  
86 a parent’s offspring, and that is likely to have originated and/or to be currently maintained for  
87 this function” (Smiseth *et al.*, 2012). The expression of parental care often has a large impact on  
88 the fitness of both parents and offspring. In particular, parental care is beneficial to offspring,  
89 because it increases their quality and/or survival by neutralizing environmental hazards (Alonso-  
90 Alvarez & Velando, 2012; Klug & Bonsall, 2014). By contrast, parental care is often costly to  
91 parents, because it reduces their condition and/or survival (for instance as the result of an  
92 increased energy loss or elevated risk of predation), and thus ultimately diminishes their lifetime  
93 reproductive success (Trivers, 1972; Alonso-Alvarez & Velando, 2012). The far-reaching  
94 consequences associated with the expression of parental care make it the core feature of family  
95 life. Shedding light onto the circumstances that allow family members to gain sufficient (indirect)  
96 benefits to offset the costs of care (cf. Hamilton, 1964; Smiseth *et al.*, 2012) has thus long been

97 considered central in the study of social life in family groups (Clutton-Brock, 1991; Gross &  
98 Clutton-Brock, 2005).

99           However, parental care is but one of many facets of family life, and only a fraction of the  
100 other facets has received close scrutiny thus far. For instance, it is well known that the expression  
101 of care can prompt evolutionary conflicts (cf. Parker, Royle, & Hartley, 2002; Royle, Hartley, &  
102 Parker, 2004) that become apparent (i) if one parent tries to reduce its parental investment at  
103 the other parent's expense (*parental antagonism*; Trivers, 1972; Lessells, 2012; Parker *et*  
104 *al.*, 2015); (ii) if offspring compete with each other for limited parental resources (*sibling rivalry*;  
105 Mock & Parker, 1997; Roulin & Dreiss, 2012); and (iii) if offspring demand more care than the  
106 parents are willing to provide (*parent-offspring conflict*; Trivers, 1974; Kilner & Hinde, 2012;  
107 Kölliker *et al.*, 2015). By contrast, processes such as sibling cooperation and parent-offspring  
108 competition only recently started to attract attention (e.g. Dreiss, Lahlah, & Roulin, 2010; Yip &  
109 Rayor, 2013; Falk *et al.*, 2014; Schrader, Jarrett, & Kilner, 2015a; Kramer *et al.*, 2017). This  
110 disparity arguably results from a strong bias toward studying family interactions in the derived  
111 social systems of birds and mammals. In these groups, young offspring are completely dependent  
112 on parental resources, and the substantial fitness effects of parental care that parallel this  
113 dependency typically prompt intense conflicts over the allocation of care (Clutton-Brock, 1991;  
114 Gross & Clutton-Brock, 2005). Derived family systems, however, only represent a small fraction  
115 of the diversity of family life in nature. Their predominance in studies of family interactions thus  
116 promotes the neglect of mechanisms that could play a greater role in less derived family systems.  
117 Moreover, the central role of parental care arguably deflects scrutiny of fitness effects that are  
118 typically masked by the benefits and costs of (conflicts over the allocation of) parental care. The

119 strong focus on parental care and its expression in altricial species hence likely distorts our  
120 understanding of the evolutionary drivers of the emergence and consolidation of family life, and  
121 could ultimately obscure their role in the (early) evolution of animal sociality.

122           Here, we advocate the direct study of family life as an integrative approach to elucidating  
123 the role of parental behaviours and other family interactions in the evolution of animal sociality.  
124 To this end, we (i) illustrate the downsides of a narrow focus on parental care by reviewing how  
125 thus far neglected types of family interaction can shape the cost-benefit ratio of family life. We  
126 then (ii) outline how accounting for these overlooked mechanisms – and their changing role in  
127 the course of evolution – could improve our understanding of the evolutionary origin and  
128 consolidation of family life. Finally, (iii) we discuss how this diachronic perspective on the  
129 evolution of family living could provide general insights into the mechanisms driving social  
130 evolution. Understanding the evolution of family life requires a complete picture of all factors  
131 that affect its fitness consequences across taxonomical groups. Albeit doubtlessly very important,  
132 parental care and its repercussions in advanced family systems only cover part of the canvas.

## 133 **II. THE SEMANTICS OF FAMILY LIFE**

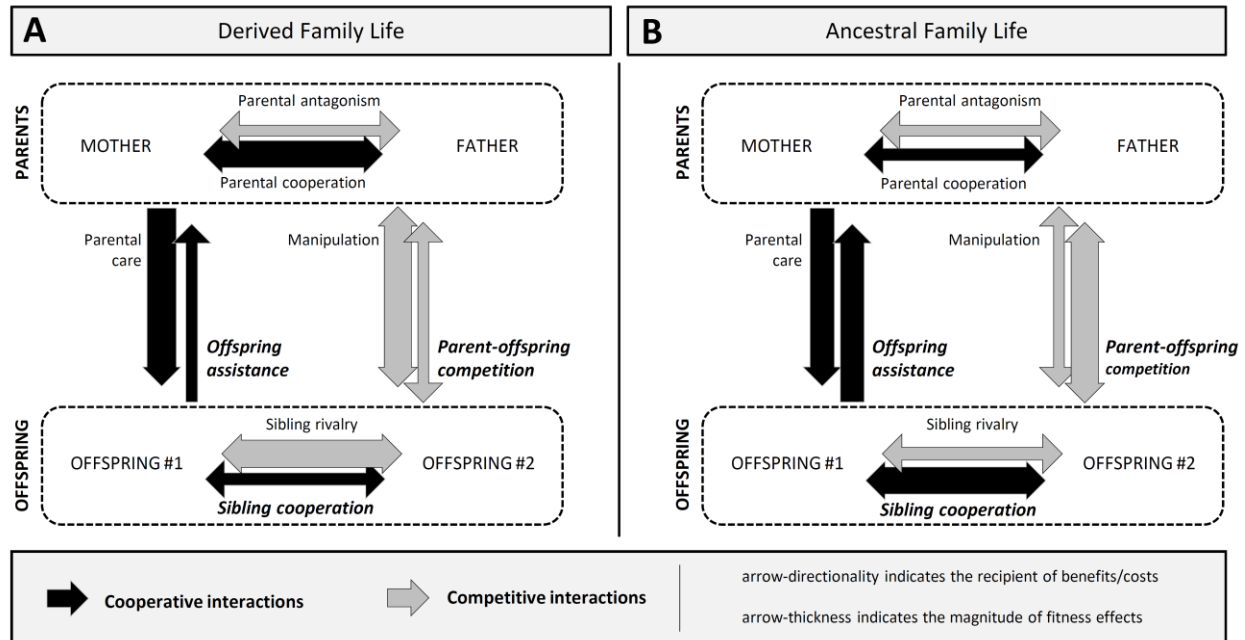
134 Somewhat surprisingly, there is no strict consensus among behavioural ecologists as to what  
135 constitutes a family. In studies on cooperative breeding, the term family is typically restricted to  
136 cases where mature offspring forgo dispersal and independent reproduction, and instead  
137 continue to interact regularly with their parents (Emlen, 1994, 1995; Covas & Griesser, 2007;  
138 Drobniak *et al.*, 2015). This narrow definition helps to identify transitional stages in the evolution  
139 of cooperative breeding (a form of family-living characterized by reproductive cooperation;

140 Drobniak *et al.*, 2015). Yet, this definition also excludes the vast diversity of (less enduring)  
141 associations between parents and their *immature* offspring. A broader meaning of the term  
142 «family» is thus frequently implied in studies on parental care (cf. Clutton-Brock, 1991; Gross &  
143 Clutton-Brock, 2005; Schrader *et al.*, 2015b; Duarte *et al.*, 2016; Jarrett *et al.*, 2017). Here, we  
144 formalize this view by defining a family as “an association of one or both caring parent(s) with  
145 their offspring”. This broad definition of the term family closely matches its colloquial meaning,  
146 and allows us to outline a general perspective that covers all types of (non-random) parent-  
147 offspring association. We suggest using more narrowly define terms such as *nuclear family* and  
148 *extended family* to delineate families of a particular composition. Specifically, we propose to use  
149 the term *nuclear family* to delineate the vast majority of family systems that consist of one or  
150 both caring parent(s) and offspring of a single reproductive attempt. Conversely, we suggest  
151 using the term *extended family* to delineate families consisting of a nuclear family and their close  
152 relatives, such that the extended family also comprises grandparents, siblings of the parents,  
153 and/or offspring of at least one additional reproductive attempt. Many societies of cooperatively  
154 breeding birds, mammals, and eusocial insects are examples of such extended families.

155       Family systems may not only differ in terms of composition, but also in terms of the extent  
156 to which parental care is integrated into offspring development. This latter difference is broadly  
157 captured by the classification into species with altricial and precocial young (from now on  
158 referred to as altricial and precocial species, respectively). In altricial species, the phenotypic  
159 integration of parental care is advanced to such an extent that juveniles cannot survive without  
160 receiving at least some care early during their life. Family life in altricial species is therefore  
161 obligatory (Clutton-Brock, 1991). Prime examples of such altricial species are found among



162 mammals, passerine birds, and eusocial insects. In precocial species, on the other hand, this  
163 phenotypic integration is limited, and offspring can survive in the absence of – nonetheless  
164 beneficial – care due to an early development of their capability to forage independently. Family  
165 life in precocial species is therefore facultative (Smiseth, Darwell, & Moore, 2003;  
166 Kölliker, 2007). Ducks, plovers, and quails, as well as many subsocial insects (such as burying  
167 beetles and earwigs) feature precocial young. Interestingly, the altricial-precocial spectrum  
168 broadly coincides with the classification into evolutionarily derived vs. non-derived family  
169 systems. In particular, altricial family systems are always derived (and derived systems typically  
170 altricial), since the high phenotypic integration of parental care characteristic of such systems  
171 only arises *after* the emergence of family life (section III.3; Kölliker, 2007; Uller, 2012).  
172 Conversely, precocial species are typically less derived (and non-derived systems are always  
173 precocial), since they feature a lower degree of phenotypic integration, and thus more closely  
174 resemble an ancestral state during which offspring were (still) largely independent of parental  
175 care (Smiseth *et al.*, 2003; Kölliker, 2007). We are aware that these dichotomic classifications  
176 only draw a rough picture of the diversity of family systems. We nevertheless retain them here,  
177 because their generality makes them useful in our discussion of the general trends shaping the  
178 evolution of family life.



179

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

### 192 **III. THE NEGLECTED FACETS OF FAMILY LIFE**

193 Family living is a form of group living. The various fitness effects inherent to all types of group-  
194 living – such as the costs of increased competition and the benefits of cooperative foraging –  
195 should therefore also occur during family life (Alexander 1974; Krause and Ruxton 2002).  
196 However, instead of investigating the full range of possible cooperative and competitive family  
197 interactions, the last decades of research on family life predominantly focused on the fitness  
198 effects of a single type of parent-offspring cooperation – parental care – as well as on the conflicts  
199 over (and the cooperation in) its allocation (see Figure 1; reviewed in Clutton-Brock, 1991; Royle,  
200 Smiseth, & Kölliker, 2012b). This implicit equalization of the fitness effects of parental care with  
201 the fitness effects of family life has led to the neglect of three potentially important dimensions  
202 of social interactions within the family: (i) sibling cooperation, (ii) parent-offspring competition,  
203 and (iii) offspring assistance (here defined as cooperative acts of offspring to the benefit of their  
204 parents). A notable exception to this general trend are studies on the highly derived, extended  
205 families of cooperative breeders, in which these mechanisms have been explored (but see section  
206 IV.2). Below, we review examples of the neglected facets of family life, and highlight that their  
207 fitness effects are often concealed by the relatively greater effects of parental care. Accounting  
208 for the effects of these mechanisms is nevertheless crucial, since they could augment or diminish  
209 the benefits and costs of parental care, and thus tip the scales in favour (or in disfavour) of the  
210 emergence and consolidation of family life.

211 **(1) Sibling cooperation**

212 Most studies of sibling interactions thus far investigated the conspicuous competitive behaviours  
213 of juvenile birds and mammals that compete over their access to limited parental resources  
214 (reviewed in Mock & Parker, 1997; Roulin & Dreiss, 2012). However, sibling interactions are not  
215 competitive by default, and an increasing number of studies report an unexpected diversity of  
216 cooperative interactions (or by-product mutualism) among altricial as well as precocial juveniles  
217 (reviewed in Roulin & Dreiss, 2012). Indeed, sibling cooperation is not only a hallmark of termite  
218 societies, where larvae, nymphs, workers and soldiers are all juveniles (Eggleton, 2011), but also  
219 occurs in the house wren *Troglodytes aedon*, where offspring postpone fledging to the benefit of  
220 their younger siblings (Bowers, Sakaluk, & Thompson, 2013); in the King Penguin *Aptenodytes*  
221 *patagonicus*, where huddling improves the juveniles' thermoregulation (Barré, 1984); in the  
222 spotted hyaena *Crocuta crocuta*, where offspring form coalitions with litter-mates against  
223 unrelated juveniles (Smale *et al.*, 1995); and in the Mississippi kite *Ictinia mississippiensis* and  
224 the ambrosia beetle *Xyleborinus saxesenii*, where offspring express mutual cleaning ('allo-  
225 preening'; Botelho, Gennaro, & Arrowood, 1993; Biedermann & Taborsky, 2011).

226 Intriguingly, juveniles can also cooperate in resource acquisition. In altricial species, such  
227 cooperation typically aims at improving the juveniles' access to parental provisioning (cf.  
228 Forbes, 2007). For instance, altricial juveniles sometimes refrain from interfering with their  
229 siblings' feeding attempts (e.g. in the blue-footed booby *Sula nebouxii*; Anderson &  
230 Ricklefs, 1995) and may even offer parentally-provided food items to their siblings (e.g. in the  
231 barn owl *Tyto alba*; Marti, 1989). Moreover, they can coordinate their begging behaviour to  
232 increase the parents' feeding rate (e.g. in the in the black-headed gull *Larus ridibundus* and the

233 banded mongoose *Mungos mungo*; Johnstone, 2004; Mathevon & Charrier, 2004; Bell, 2007),  
234 or negotiate their share of parental resources to avoid the greater costs of unrestrained sibling  
235 rivalry (e.g. in the barn owl *T. alba*, the spotless starling *Sturnus unicolor* and the meerkat *Suricata*  
236 *suricatta*; Roulin, 2002; Johnstone & Roulin, 2003; Bulmer, Celis, & Gil, 2008; Madden *et*  
237 *al.*, 2009; Dreiss *et al.*, 2010). By contrast, cooperation in resource acquisition among precocial  
238 juveniles can – at least in principle – occur independently of parental provisioning. For instance,  
239 food sharing occurs even without parental involvement in the European earwig *Forficula*  
240 *auricularia* (Falk *et al.*, 2014; Kramer, Thesing, & Meunier, 2015) and in many social spiders such  
241 as the huntsman spider *Delena cancerides* (Yip & Rayor, 2013, 2014).

242         In both altricial and precocial species, the fitness effects of sibling cooperation might  
243 often be concealed by the effects of parental care. In line with this assumption, it has recently  
244 been shown that larval mass in the burying beetle *Nicrophorus vespilloides* peaks at a higher  
245 larval density in the absence of care. This suggests that parental care usually masks the beneficial  
246 effect of initial increases in larval density on the brood's ability to penetrate and use the breeding  
247 carcass (Schrader *et al.*, 2015a). This notwithstanding, the diverse forms and broad taxonomical  
248 distribution of cooperative behaviours among juveniles suggest that sibling cooperation is not  
249 only important during the adult life stage (cf. Wilson, 1971; Clutton-Brock, 1991; Koenig &  
250 Dickinson, 2004), but might also play a crucial role in the evolution of family life (see section III).

## 251 **(2) Parent-offspring competition**

252 Competition between parents and their offspring occurs whenever the consumption of an  
253 essential resource by the parents limits the availability of this resource to their offspring – or vice

254 versa. This form of kin competition typically arises with the onset of offspring foraging, and has  
255 been predicted to promote offspring dispersal and thus the breakup of family units (Hamilton &  
256 May, 1977; Comins, Hamilton, & May, 1980; West, Pen, & Griffin, 2002). Direct evidence for  
257 these effects in altricial species is as yet scarce. However, experimental food removal in the  
258 western bluebird *Sialia mexicana* reduced the number of sons that remained with their parents  
259 until after winter, suggesting that parent-offspring competition can indeed promote the breakup  
260 of family units (Dickinson & McGowan, 2005). Similarly, food supplementation delayed offspring  
261 dispersal in the carrion crow *Corvus corone corone*, indicating that parent-offspring competition  
262 could select against the evolution of cooperative breeding (Baglione *et al.*, 2006). In further  
263 support of this notion, resource depletion during the breeding season likely leads to competition  
264 between breeders and helpers in the chestnut-crowned babbler *Pomatostomus ruficeps*, and  
265 thus overall increases the costs of group-living (Sorato, Griffith, & Russell, 2016).

266 In analogy to its effects in altricial species, parent-offspring competition can also affect  
267 offspring dispersal and the duration of family life in precocial species. For instance, parent-  
268 offspring competition has been shown to promote offspring dispersal in the solitary common  
269 lizard *Lacerta vivipara* (Léna *et al.*, 1998; Le Galliard, Ferrière, & Clobert, 2003; Cote, Clobert, &  
270 Fitze, 2007). Conversely, the prolonged presence of fathers has been shown to reduce offspring  
271 survival under food limitation in *N. vespilloides*, a burying beetle with biparental care in which  
272 both parents feed on the breeding carcass (Scott & Gladstein 1993; Boncoraglio & Kilner 2012).  
273 This latter finding suggests that father-offspring competition might offset the benefits of paternal  
274 care, and thus offers a potential explanation as to why fathers typically leave the brood earlier  
275 than mothers in this species. Intriguingly, parent-offspring competition in precocial species might

276 even entirely negate the benefits of family living under certain harsh conditions. In line with this  
277 hypothesis, mother-offspring competition under food limitation has been shown to render  
278 maternal presence detrimental to offspring survival in uniparental families of the European  
279 earwig *F. auricularia* (Meunier & Kölliker, 2012; Kramer *et al.*, 2017).

280         Particularly in precocial species, such costs of parent-offspring competition are likely  
281 often concealed by the benefits of parental care. Indeed, carcasses guarded by *N. vespilloides*  
282 fathers are less likely to be taken over by conspecifics, suggesting that the costs of father-  
283 offspring competition are typically offset by the benefits of offspring defence against infanticide  
284 through conspecifics (Scott & Gladstein, 1993). Similar benefits of parental care might also  
285 explain why *F. auricularia* offspring do not disperse earlier under resource limitation (Wong &  
286 Kölliker, 2012). Finally, note that such masking effect of parental care are likely less pronounced  
287 in altricial species, since the benefits of parental care often decrease towards the end of family  
288 life (cf. Bateson, 1994), and will thus often be limited once parent-offspring competition arises.  
289 Given its early onset and multifaceted role in precocial species, parent-offspring competition  
290 might play a crucial role in the evolution of family life (see section III).

### 291 **(3) Offspring assistance**

292 Cooperation between parents and their offspring is prominently featured in a plethora of studies  
293 on parental care (reviewed in Clutton-Brock, 1991; Royle *et al.*, 2012b). However, parent-  
294 offspring cooperation is not a one-way road and can also involve cooperative behaviours (or by-  
295 product mutualism) that offspring direct towards their parents. Such *offspring assistance* is  
296 pervasive in the extended families of cooperative breeders, where adult offspring often assist

297 their parents in raising younger siblings (Wilson, 1971; Bourke & Franks, 1995; Cockburn, 1998;  
298 Koenig & Dickinson, 2016). Yet offspring assistance during family life can also be performed by  
299 juveniles. Among altricial species, it frequently occurs in eusocial insects where larvae/nymphs  
300 can fulfil crucial roles for colony functioning (reviewed in Eggleton, 2011; Schultner, Oettler, &  
301 Helanterä, 2017), for instance by defending the colony – and thus the reproductives – as soldiers  
302 (in virtually all termites; (Howard & Thorne, 2011); by taking over gallery extension and the  
303 compressing of waste into compact balls (in the ambrosia beetle *X. saxesenii*; Biedermann &  
304 Taborsky, 2011); or by acting as “communal stomach” (cf. Wheeler, 1918; Dussutour &  
305 Simpson, 2009) that provisions the queen with secretions necessary for protein degradation (in  
306 the metricus paper wasp *Polistes metricus*; Hunt, 1984) or sustained egg production (in pharaoh  
307 ant *Monomorium pharaonis*; Børgesen, 1989; Børgesen & Jensen, 1995).

308         Apart from its role in altricial species with highly complex societal organization, the notion  
309 of offspring assistance has received little attention. However, recent findings indicate that  
310 parents can also benefit from offspring assistance in precocial species. For instance, parents  
311 might benefit from their offspring’s investment into shared immune traits (*social immunity*;  
312 Cremer, Armitage, & Schmid-Hempel, 2007; Meunier, 2015), independent foraging, or defence  
313 against predation (Krause & Ruxton, 2002). In line with the former notion, faeces of caring  
314 mothers exhibit a lower antifungal activity than those of non-caring females in the European  
315 earwig *F. auricularia*, suggesting that mothers might downregulate or at least not compensate  
316 for the reduction in their own investment into nest sanitation during family life, and instead rely  
317 on the superior antifungal properties of the faeces of their juveniles (Diehl *et al.*, 2015).  
318 Conversely, delayed juvenile dispersal improves the survival of tending mothers in the subsocial



319 spider *Anelosimus studiosus* (Jones & Parker, 2002), a finding that might reflect benefits of  
320 offspring investment into prey capture or into the maintenance of the communal web. Indeed,  
321 offspring assist in web construction in many social spiders (Yip & Rayor, 2014), suggesting that  
322 mothers could regularly benefit by reducing their own investment. Although such benefits of  
323 offspring assistance for parents might be concealed by the costs of parental care, they could  
324 nevertheless have a significant impact on the evolution of family interactions and, more  
325 generally, on the emergence of social life in family units (see section III). Investigating the role of  
326 offspring assistance and the other neglected facets of family life is thus crucial to advance our  
327 understanding of the evolution of social life in family groups.

### 328 **III. THE (EARLY) EVOLUTION OF FAMILY LIFE**

329 The evolution of family life generally presumes that the fitness benefits of family living outweigh  
330 the costs of a prolonged association of the family members (Alexander, 1974; Clutton-Brock,  
331 1991; Klug et al., 2012). However, the impact of the processes mediating these benefits can  
332 change over evolutionary time (Smiseth *et al.*, 2003; Falk *et al.*, 2014; Royle, Alonzo, &  
333 Moore, 2016). This is because the current benefits associated with a trait (such as a parental  
334 behaviour) do not necessarily reflect the adaptive value of this trait in an ancestral state  
335 (Williams, 1966). For instance, the high benefits associated with parental food provisioning in  
336 derived family systems typically reflect the dependency of offspring on food provided by the  
337 parents, a state that only evolved *after* the emergence of parental provisioning. The benefits of  
338 parental provisioning are thus likely less pronounced in non-derived family systems (Smiseth *et*  
339 *al.*, 2003; Klug *et al.*, 2012; Royle *et al.*, 2012a). Conversely, mechanisms playing a limited role

340 in derived systems might have a more prominent role in less derived systems (section III.2.b).  
341 Understanding the evolution of family living therefore requires a complete picture of the  
342 mechanisms promoting family life in both derived and non-derived family systems.

343         However, instead of investigating the full range of mechanisms across different family  
344 systems, the last decades of empirical research mostly focused on investigating the current  
345 benefits and costs of parental care in the derived family systems of altricial vertebrates (reviewed  
346 in Clutton-Brock, 1991; Royle *et al.*, 2012b). By contrast, the fitness effects of family interactions  
347 in precocial species, which feature facultative forms of family life reminiscent of an ancestral  
348 state, have received comparably little attention (but see, for instance, Eggert, Reinking, &  
349 Müller, 1998; Zink, 2003; Salomon, Schneider, & Lubin, 2005; Kölliker, 2007). Similarly,  
350 theoretical approaches have thus far only indirectly explored the evolution of family life, since  
351 they typically investigated the influence of life-history characteristics, co-evolutionary dynamics,  
352 or environmental conditions on the evolutionary origin and maintenance of parental care  
353 (Wilson, 1975; Tallamy, 1984; Tallamy & Wood, 1986; Bonsall & Klug, 2011a; Klug *et al.*, 2012).  
354 As a corollary of this narrow focus on parental care, our current understanding of the early  
355 evolution of family life remains fragmentary. In the following section, we address this  
356 fundamental issue. Specifically, we review the factors promoting the emergence and subsequent  
357 consolidation of family life, and demonstrate that integrating the costs and benefits of thus far  
358 overlooked facets of family life in particular – and the study of precocial family systems in general  
359 – could entail major changes in our understanding of the evolution of family life.

360 **(1) The emergence of family life**

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

362 The evolutionary emergence of family life has typically been explored indirectly in studies  
363 endeavouring to understand which factors favoured the extension of pre-hatching parental care  
364 beyond the time of offspring emergence (e.g. Lack 1968; Clutton-Brock 1991; Smiseth et al.  
365 2012). These studies suggest that the emergence of parental care – and thus family life – requires  
366 the concurrence of factors that jointly make sustained social interactions among family members  
367 possible and – should the occasion arise – able to spread in the population (Klug *et al.*, 2012).  
368 The initial step in the emergence of family life is promoted by life-history characteristics ensuring  
369 that social behaviours are primarily directed toward family members (Tallamy & Wood, 1986;  
370 Lion & van Baalen, 2007). This propensity to mainly interact with family members increases the  
371 scope for the evolution of cooperative behaviours (such as parental care and sibling cooperation)  
372 by reducing the likelihood that such behaviours are misdirected toward non-kin (Hamilton, 1964;  
373 Lion & van Baalen, 2007). Hence, family life is most likely to emerge if parents and offspring  
374 recognize each other (e.g. by means of kin or familiarity recognition; cf. Evans 1998; Fellowes  
375 1998; Dobler and Kölliker 2011) or if they frequently encounter each other (e.g. due to limited  
376 dispersal; Hamilton 1964a; Lion and van Baalen 2007). Additionally, the emergence of family life  
377 can be promoted by the presence of precursors of post-hatching care (Tallamy & Wood, 1986;  
378 Royle *et al.*, 2012a). In line with this idea, the evolution of offspring attendance and guarding in  
379 cooperative breeders has been suggested to derive from ancestral defensive or aggressive  
380 behaviours (Tallamy, 1984). Similarly, parental provisioning during family life might have evolved  
381 via selection acting on – and modifying – self-feeding behaviours (Cunningham *et al.*, 2016), and

382 some effector molecules in social immunity might have been recruited from a function in  
383 personal immunity (Palmer *et al.*, 2016).

384         Once the preconditions for the emergence of family life are met, effects of (additional)  
385 life-history characteristics and environmental conditions jointly determine whether it can spread  
386 in the population against the background of the prevalent solitary lifestyle (Tallamy, 1984;  
387 Clutton-Brock, 1991; Klug *et al.*, 2012). In particular, environmental conditions – including the  
388 spatial and temporal availability of limited resources and the presence of predators or parasites  
389 (reviewed in Wilson, 1975; Krause & Ruxton, 2002; Botterill-James *et al.*, 2016; see also  
390 Botterill-James *et al.*, 2016) – typically modify the impact of basic life-history conditions (such as  
391 stage-specific mortality and maturation rates) on the benefits and costs of family interactions  
392 (Bonsall & Klug, 2011a; Klug *et al.*, 2012). For instance, harsh conditions and the concomitant  
393 intense competition for limited resources have been predicted to increase the mortality rate of  
394 solitary individuals (Wilson, 1975; Clutton-Brock, 1991). This, in turn, should promote the  
395 evolution of parental care and thus family life, because the uncertain prospects of future  
396 reproduction decrease the relative costs of care to adults (Klug & Bonsall, 2010; Bonsall &  
397 Klug, 2011a), and increase its potential benefits to offspring (Webb *et al.*, 2002; Klug &  
398 Bonsall, 2010). However, empirical findings are sometimes at odds with these predictions. For  
399 instance, harsh conditions negate rather than increase the usual benefits of maternal presence  
400 and thus family life in the European earwig *F. auricularia* (Meunier & Kölliker, 2012; Kramer *et*  
401 *al.*, 2017). The limited predictive power of the standard account of the evolution of family life  
402 (cf. Costa, 2006; Trumbo, 2012; Capodeanu-Nägler *et al.*, 2016) might partly reflect that  
403 environmental conditions, life-history characteristics, and the benefits and costs of parental care

404 often interact in unexpected ways (Bonsall & Klug, 2011a, 2011b; Meunier & Kölliker, 2012).  
405 However, we believe that it also reflects an excessive focus on a subset of family interactions,  
406 and their expression in a subset of family systems.

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

408 The standard account for the evolutionary origin of family life solely focuses on the extension of  
409 parental care beyond offspring emergence, and thus inadvertently neglects the role of other  
410 social interactions within the nascent family. However, these neglected facets could have a  
411 profound influence on family life. In particular, parent-offspring competition (and its potential  
412 knock-on effects on sibling rivalry and parental antagonism) could impede the evolution of family  
413 life by reducing the potential benefits of care (Meunier & Kölliker, 2012; Kramer *et al.*, 2017).  
414 Conversely, both sibling cooperation and offspring assistance could promote the emergence of  
415 family living by, respectively, augmenting the (initially limited) benefits of care to offspring, and  
416 offsetting some of its costs to parents (cf. Falk *et al.*, 2014; Kramer *et al.*, 2015). For instance,  
417 sibling cooperation during foraging could promote reciprocal food sharing (such as in the vampire  
418 bat *Desmodus rotundus*; Wilkinson, 1984; Carter & Wilkinson, 2013), and thus provide a  
419 mechanism for insurance against variability (Koenig & Walters, 2015). Intriguingly, these forms  
420 of cooperation could themselves evolve from by-product benefits (such as predator dilution  
421 effects; Krause & Ruxton, 2002) arising in offspring aggregations.

422 The benefits of by-product mutualism or sibling cooperation in such offspring  
423 aggregations could also affect the initial duration of family life. In particular, they could offer an  
424 additional incentive (or even an alternative reason; see section IV.1) for offspring to delay

425 dispersal from their natal site (Kramer *et al.*, 2015), and might thus allow extended periods of  
426 family life right from the start. This scenario contrast with the standard account for the evolution  
427 of family life, where the “simple” extension of parental care beyond offspring emergence (cf.  
428 Michener, 1969; Costa, 2006) should initially only allow for brief periods of family life. This is  
429 because the standard account neglects the potential impact of cooperation among offspring, and  
430 thus implies that offspring in recently evolved family systems should (still) tend to disperse soon  
431 after hatching to avoid the impending competition with their siblings and parents (West *et*  
432 *al.*, 2001, 2002). Longer periods of family-living would only arise secondarily, where the benefits  
433 of offspring attendance and other early forms of parental care select for delayed offspring  
434 dispersal. From an offspring’s point of view, family life is classically thought to evolve *despite of*  
435 the presence of competing siblings (cf. Mock & Parker, 1997; Roulin & Dreiss, 2012). However,  
436 the occurrence and potential role of sibling cooperation suggests that family life might rather  
437 emerge – or at least be initially favoured – *because of* the presence of siblings.

438         Similar to the fitness effects of early forms of parental care (see section III.1.a), the impact  
439 of other facets of family life likely depends on life-history characteristics and the prevailing  
440 environmental conditions. Costs of parent-offspring competition, for instance, will be greatest if  
441 parents and offspring feed on the same resources, and simultaneously forage in the same area.  
442 Conversely, the benefits of sibling cooperation might be greatest if offspring forage  
443 independently of each other, since this would decrease sibling rivalry (cf. Mock & Parker, 1997),  
444 and thus increase the incentive of juveniles to cooperate with each other (Frank, 1998, 2003).  
445 Finally, the possible spectrum of different types of sibling cooperation and offspring assistance is  
446 likely subject to developmental constraints (cf. Maynard Smith *et al.*, 1985), where certain types

447 of behaviours cannot be performed effectively by immatures. Besides these life-history traits, the  
448 (environmentally determined) availability of limited resources is likely a crucial factor shaping the  
449 fitness effects of the neglected facets of family life. This is because resource limitation would  
450 both increase the scope for parent-offspring competition, and decrease the propensity of  
451 juveniles to cooperate with their siblings or parents (West *et al.*, 2002; Frank, 2003; see also  
452 section III.2.b). Such harsh conditions might thus hamper the evolution of family life despite the  
453 expected high benefits of parental care (Webb *et al.*, 2002; Klug & Bonsall, 2010). Overall, such  
454 as yet poorly explored effects might help explaining why even closely related species exposed to  
455 ostensibly identical conditions often differ in the occurrence and nature of family interactions (cf.  
456 Costa, 2006; Trumbo, 2012; Capodeanu-Nägler *et al.*, 2016).

## 457 **(2) The consolidation of family life**

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

459 After the emergence of family units, coevolutionary feedback-loops between parental and  
460 offspring traits are expected to promote the evolution and diversification of parental care, and  
461 thus to lead to the rapid consolidation of family life (Wolf, Brodie III, & Moore, 1999; Kölliker,  
462 Royle, & Smiseth, 2012; Uller, 2012; Jarrett *et al.*, 2017). For instance, the initial evolution of  
463 parental provisioning may trigger evolutionary changes in other components of care as well as in  
464 offspring traits, allowing parents to choose safer nest sites, but also increasing the competition  
465 among offspring for parentally provided food. This increased sibling rivalry may, in turn, further  
466 advance the evolution of parental provisioning, thereby closing the coevolutionary feedback-  
467 loop between parental provisioning, the choice of safer nest sites, and sibling rivalry (Smiseth,

468 Lennox, & Moore, 2007; Gardner & Smiseth, 2011). Such mutual reinforcement between  
469 parental and offspring traits has been predicted to promote a unidirectional trend from simple  
470 ancestral forms toward complex forms of family life by fostering an increasingly tight phenotypic  
471 integration of parental care and offspring development (Wilson, 1975; Gardner &  
472 Smiseth, 2011; Kölliker *et al.*, 2012; Uller, 2012; Royle *et al.*, 2016). In the highly-derived family  
473 systems of altricial species, this phenotypic integration is advanced to such an extent that  
474 juveniles cannot survive without at least some care early in their life (Kölliker, 2007; Uller, 2012).

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

476 The increasingly tight integration of parental care into offspring development that evolves during  
477 the consolidation of family life could have a profound effect on the relative importance of the  
478 neglected facets of family life. For instance, the evolution of parental provisioning and the  
479 concomitant increased reliance of offspring on parentally provided food likely leads to a delayed  
480 onset of offspring foraging (cf. Gardner & Smiseth, 2011), and should thus reduce the scope for  
481 competition between parents and their offspring. As a result, the impact of parent-offspring  
482 competition on family dynamics might steadily decline in the course of the consolidation of family  
483 life (Kramer *et al.*, 2017). Similarly, siblings might be most likely to cooperate with each other as  
484 long as they are (still) largely independent of parental care. This is because an increased  
485 dependency on care is typically paralleled by increased sibling rivalry (Gardner & Smiseth, 2011),  
486 and should thus decrease the levels of sibling cooperation (Frank, 1998, 2003). Finally, an  
487 increased offspring dependency is likely also accompanied by greater developmental constraints  
488 (cf. Maynard Smith *et al.*, 1985) on the type of social behaviours that the immature juveniles can



489 perform, suggesting that both sibling cooperation and offspring assistance might occur less  
490 frequently in altricial than in precocial species. Overall, these considerations indicate that parent-  
491 offspring competition, sibling cooperation, and offspring assistance might fulfil crucial roles in  
492 ancestral family systems, but could lose ground where the consolidation of family life promotes  
493 an increasingly tight phenotypic integration of parental care into offspring development.

494         While the role of parent-offspring competition, sibling cooperation, and offspring  
495 assistance in nuclear families thus far received little attention, their impact on the evolution of  
496 the extended families of cooperative breeders has been more thoroughly explored (e.g. Bourke  
497 & Franks, 1995; Baglione *et al.*, 2006; Koenig & Dickinson, 2016; Sorato *et al.*, 2016).  
498 Interestingly, all three facets play a prominent role in shaping these systems: parent-offspring  
499 competition can impede the evolution of cooperative breeding (Baglione *et al.*, 2006; Sorato *et*  
500 *al.*, 2016), siblings within breeding groups frequently cooperate with each other (e.g. during  
501 group foraging or in the defence against predation), and offspring assistance in the form of  
502 alloparental care (often called ‘help’) is the very foundation of cooperative breeding  
503 (Skutch, 1935; Cockburn, 1998; Koenig & Dickinson, 2016). However, while these mechanisms  
504 usually involve juveniles in nuclear families, they typically involve adult offspring in cooperative  
505 breeders. Notably, the resurgence of these mechanisms in cooperative breeders after their  
506 demise during the consolidation of (nuclear) family life is in line with a key role of offspring  
507 dependency in determining their occurrence. Like juveniles in ancestral family systems, adult  
508 offspring in cooperative breeders are largely independent of parental care, a situation that not  
509 only promotes parent-offspring competition, but also shifts competition towards a  
510 global(population-wide) scale (cf. West *et al.*, 2002), and thus prevents the high levels of sibling

511 rivalry that usually reduce the likelihood that sibling cooperation and offspring assistance occur  
512 (see above). The putatively similar role of these mechanisms in ancestral and cooperatively  
513 breeding families suggests that the extensive literature on the evolution of cooperative breeding  
514 could inform studies of the emergence of family life from a solitary state. In particular, the  
515 distinction between a helper's decision to stay and its subsequent decision to provide  
516 alloparental care (e.g. Ekman & Tegelström, 1994; Griesser *et al.*, 2017) could be applied to the  
517 evolution of family units, and might then suggest that the initial formation of family units is not  
518 necessarily (only) driven by the benefits of parental care (see also section IV.1).

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

520 Far from being restricted to elucidating the role of the three neglected facets of family life, the  
521 study of family interactions in precocial species can also shed light on other aspects of the  
522 evolution of family living. For instance, it might help explaining why simple family life still abounds  
523 across taxa (e.g. Tallamy & Schaefer, 1997; Lin, Danforth, & Wood, 2004; Filippi *et al.*, 2009)  
524 despite the expected trend towards complex family systems (Wilson, 1975; Gardner &  
525 Smiseth, 2011; Kölliker *et al.*, 2012; Uller, 2012; Royle *et al.*, 2016). In general terms, this  
526 mismatch between theoretical expectations and empirical findings indicates that some as yet  
527 unknown factors counteract the consolidation of family life and thus prevent an increase in social  
528 complexity. We recently showed that long-term and transgenerational costs of parental loss  
529 (such as an impaired development of juveniles) are not restricted to altricial family systems (e.g.  
530 Harlow & Suomi, 1971; Gonzalez *et al.*, 2001; Fleming *et al.*, 2002; Andres *et al.*, 2013), but can  
531 also occur in precocial species (Thesing *et al.*, 2015). This finding suggests that the mortality rate

532 of parents *during* family life could be one of the factors counteracting its consolidation. This is  
533 because even though precocial juveniles can survive the early death of their parents, they will  
534 still suffer (non-lethal) consequences of parental loss. Accordingly, high parental mortality rates  
535 might not only increase the likelihood that these negative consequences arise; rather, they might  
536 also select against the further consolidation of family life, since the concomitant deepened  
537 integration of parental care into offspring development would increase the costs of parental loss.  
538 Similarly, the consolidation of family life might be hindered where (variation in) the availability  
539 of limited resources prevents parents from reliably provisioning their offspring. Such situations  
540 could also select for the maintenance of alternative survival strategies among juveniles  
541 (Kölliker, 2007; Kramer *et al.*, 2015; Kramer & Meunier, 2016a). We surmise that the reliability  
542 of parental care – i.e. the likelihood that offspring indeed receive care once it has originated –  
543 will prove crucial in determining whether a given family system evolves towards increasing  
544 complexity (see also Capodeanu-Nägler *et al.*, 2016).

545         Advanced family systems are typically caught in a *parental trap* that enforces the  
546 maintenance of family life irrespective of its current adaptive value (Eberhard, 1975). By  
547 contrast, less derived forms of family life can be lost over evolutionary times (Tallamy &  
548 Schaefer, 1997; Lin *et al.*, 2004; Filippi *et al.*, 2009). In the light of the above considerations, this  
549 contrast indicates the existence of a threshold of social complexity that determines whether  
550 family life is self-sustaining. Above this threshold, the phenotypic integration of parental care  
551 into offspring development would be tight enough to render parental care obligatory for  
552 offspring survival. Family life would then be beneficial to offspring irrespective of the external  
553 conditions, and could thus hardly ever be lost. By contrast, the integration of parental care into

554 offspring development below this threshold would be sufficiently limited to enable offspring  
555 survival in the absence of the parents. In this situation, family life would remain facultative, and  
556 the interplay between environmental conditions, life-history characteristics and the costs-benefit  
557 ratio of all types of family interactions would determine whether family life is maintained at its  
558 *status quo*, abandoned in favour of a solitary lifestyle, or propelled towards the threshold that  
559 separates facultative from obligatory family systems. The existence of a similar threshold (or  
560 *point of no return*) has been invoked to explain the transition from facultative to obligatory  
561 eusociality (Wilson & Hölldobler, 2005). With regard to the evolution of family life, such a  
562 threshold would reconcile the current debate over the loss of parental care and family life (cf.  
563 Trumbo, 2012), since it allows for the co-existence of stable as well as unstable family systems.  
564 It would also leave scope for the theoretically expected unidirectional trend toward increasingly  
565 complex family systems – namely if the prevailing conditions are favourable and stable enough  
566 to promote an ever-increasing integration of parental and offspring traits.

#### 567 **IV. IMPLICATIONS FOR SOCIAL EVOLUTION**

568 Throughout the history of life on earth, previously independent units (such as cells) have formed  
569 social collectives (such as multicellular organisms) to cope with the challenges imposed by their  
570 changing environment. Transitions from solitary to social life were the incipient steps in such  
571 *major transitions* in evolution, and hence often had far-reaching repercussions on the diversity,  
572 complexity, and hierarchical organization of life itself (Maynard Smith & Szathmáry, 1995;  
573 Bourke, 2011). Indeed, the quest for general mechanism driving such transitions has  
574 preoccupied scientists ever since Charles R. Darwin (Darwin, 1859) first speculated on the

575 evolution of eusocial societies (cf. Alexander, 1974; Krause & Ruxton, 2002; Bourke, 2011).  
576 Since then, the mechanisms driving transitions from simpler social systems to the highly  
577 integrated and often permanent societies of cooperatively breeding vertebrates and eusocial  
578 insects have been thoroughly explored (e.g. Wilson, 1971; Bourke & Franks, 1995; Crozier &  
579 Pamilo, 1996; Koenig & Dickinson, 2004, 2016). The evolutionary origin of the simpler social  
580 systems themselves, however, has received less attention (Trumbo, 2012; Falk *et al.*, 2014; van  
581 Gestel & Tarnita, 2017; Boomsma & Gawne, 2017), and the mechanisms promoting the early  
582 evolution of social life remain poorly understood. The emergence of family living exemplifies a  
583 transition from solitary to social life, and marks the origin of an (initially) simple social system.  
584 Moreover, it constitutes the initial step towards the major transition to eusociality (Maynard  
585 Smith & Szathmary, 1995; Bourke, 2011; Boomsma & Gawne, 2017). Understanding the origin  
586 and consolidation of family life might thus help to shed light on processes that also shape (the  
587 early steps of) other evolutionary transitions (see also van Gestel & Tarnita, 2017). In the  
588 following part, we discuss how adopting a broad perspective on the evolution of family life could  
589 provide general insights into the factors shaping social evolution.

### 590 **(1) Pathways to group formation**

591 Social interactions among juveniles likely have a crucial impact on the early evolution of family  
592 units (see section III.1.b); yet their impact could go beyond the simple reinforcement of the  
593 benefits of parental care. In particular, the benefits of such interactions might influence the initial  
594 formation of family units, and could thus have implications for our understanding of the  
595 pathways to group formation. The transition to group-living is generally envisioned to follow

596 either the semisocial or the subsocial pathway (Michener, 1969; Bourke, 2011). The semisocial  
597 pathway occurs when group formation results from the aggregation of individuals of the same  
598 generation, a process that, for instance, gave rise to the larval societies of sawflies and colonies  
599 of communally nesting halictid bees (Michener, 1969; Costa, 2006; Bourke, 2011). By contrast,  
600 the subsocial pathway occurs when group formation results from the association of parents with  
601 their offspring, an event that corresponds to the emergence of social interactions among the  
602 family members (Queller, 2000; Bourke, 2011), and ultimately gave rise to the majority of  
603 advanced animal societies (Wheeler, 1928; Wilson, 1975; Bourke, 2011; Boomsma &  
604 Gawne, 2017). Interestingly, the potential role of sibling cooperation during early stages of the  
605 evolution of family life (see section III.2.b) suggests that aggregations of juveniles might not only  
606 constitute an alternative (semisocial) pathway to group formation; rather, they could actually  
607 precede the emergence of (subsocial) family life. Specifically, semisocial aggregations of juveniles  
608 could initially arise whenever the benefits of sibling interactions favour delayed dispersal, and  
609 might subsequently give rise to families if parents extend already existing forms of pre-hatching  
610 care beyond offspring emergence (e.g. Lack, 1968; Clutton-Brock, 1991; Smiseth *et al.*, 2012).  
611 This scenario suggests that species might not only exhibit both the subsocial and the semisocial  
612 pathway to group formation during different stages of their life cycle (Costa, 2006); rather, they  
613 might follow the two pathways at different times in the course of their evolutionary history.

## 614 **(2) The rise and fall of cooperation and conflict**

615 In the course of major evolutionary transitions, cooperation typically spreads among lower-level  
616 units (such as individuals in the transition to eusociality) and replaces the initially prevailing

617 conflicts between them (Bourke, 2011). The evolution of family life shows evidence for both  
618 processes: parental care, a hallmark cooperative trait (Hamilton, 1964; Smiseth *et al.*, 2012),  
619 greatly diversifies during the evolution of complex family systems. Conversely, the initially  
620 prevailing direct competition between parents and offspring might be progressively suppressed  
621 (Kramer *et al.*, 2017). However, the evolutionary dynamics shaping family living also indicate that  
622 not all forms of cooperation might be favoured and not all conflicts equally suppressed during its  
623 consolidation. For instance, cooperation among juvenile siblings might occur frequently in  
624 facultative family systems, but is arguably rare in advanced systems with obligatory family life  
625 (Roulin & Dreiss, 2012; Kramer *et al.*, 2015). Conversely, sibling rivalry and parent-offspring  
626 conflict (*sensu* Trivers, 1974) typically increase during the evolution of complex family systems  
627 (Gardner & Smiseth, 2011). These findings suggest that some conflicts that are characteristic of  
628 later stages in an evolutionary transition might arise from dynamics that shaped earlier stages of  
629 that transition. In more general terms, they indicate that the increase in cooperation and the  
630 suppression of conflicts might be overall trends that need to hold true neither for all types of  
631 cooperation and conflict, nor for all stages of a transition. Notably, social systems might evolve  
632 towards a major transition even if a specific form of cooperation [such as sibling cooperation] is  
633 lost – namely if its benefits are offset by the benefits of a simultaneous increase in another form  
634 of cooperation [such as parental care] and/or the reduction in the costs of some form of conflict  
635 [such as parent-offspring competition].

### 636 **(3) The consolidation of social life**

637 The various stages of a major transition broadly fall into two categories describing the initial  
638 formation of *collectives* (such as groups) out of formerly independent *particles* (such as  
639 individuals) on the one hand, and the subsequent transformation of these collectives on the  
640 other hand (Bourke, 2011). This transformational phase entails the transfer of key (e.g.  
641 metabolic or reproductive) functions from the particle to the collective level (Maynard Smith &  
642 Szathmáry, 1995; Bourke, 2011), and hence exhibits a striking resemblance to the consolidation  
643 of family life. In both cases, an increasingly tight phenotypic integration ties the fate of single  
644 particles [offspring] closer and closer to the fate of the collective [family], eventually resulting in  
645 obligatory social life – that is the inability of particles [offspring] to survive alone. This  
646 resemblance suggests that the reliability with which particles can derive benefits from the  
647 collective might have a crucial role in the transformational phase that corresponds to the role of  
648 the reliability of parental care in the consolidation of family life (see section III.2.c). For instance,  
649 the likelihood of a costly collapse of a facultative collective (i.e. the likelihood of ‘collective  
650 mortality’) might influence whether the phenotypic integration among its constituent particles  
651 proceeds, and could thus ultimately determine whether the collective becomes obligatory for  
652 particle-survival. Like the shift from facultative to obligatory family life, the shift from facultative  
653 to obligatory collectives could occur when environmental conditions and life-history  
654 characteristics of the particles allow for the breaching of a threshold of social complexity (see  
655 section III.2.b). Interestingly, the increasing phenotypic integration among the particles  
656 underlying this shift might also be paralleled by a shift from particle to collective-level selection  
657 (Okasha, 2005; Shelton & Michod, 2010). This change in the most relevant level of selection



658 could in turn determine whether kin selection or multilevel selection approaches best describe  
659 the underlying evolutionary process (Kramer & Meunier, 2016b; Okasha, 2016). The different  
660 stages of the evolution of family life offer rich opportunities to investigate these possibilities.  
661 Exploring the intricacies of family life might thus be a good starting point to advance our  
662 understanding of the major transitions and the theoretical framework of sociobiology.

## 663 **VI. CONCLUSIONS**

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

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

678 assistance. We suggested that the impact of these facets is often – and especially in derived  
679 family systems – concealed by the fitness effects of parental care.

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

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

695 (5) Finally, we discuss how diachronic perspective on the evolution of family living could provide  
696 novel insights into the mechanisms driving social evolution. In particular, we suggest that  
697 (subsocial) family life can evolve secondarily from semisocial aggregations of juveniles that delay  
698 dispersal to reap the benefits of sibling cooperation. We argue that the role of the reliability of

699 the benefits of parental care in the consolidation of family life can be generalized, which would  
700 suggest a key role of the reliability of ‘collective’ benefits in the consolidation of social life.

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

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