Co-evolution, conflict and complexity: what have we learned about the evolution of parental care behaviours?

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Care is complex but recent advances are helping to unravel this complexity. The factors that promote the evolutionary origins of care and those promoting the subsequent evolution, diversification and maintenance of care are not the same. Theoretical and empirical research suggest that the origin of parental care will depend primarily on offspring survival in the absence of care, as long as there are appropriate behavioural precursors and genetic co-variation between parent and offspring behaviours for care to evolve. In contrast, which sex cares and how much care is provided is shaped by a suite of related factors that affect how the behaviour of family members co-evolves, including adult mortality rates, parentage, sexual selection and mechanisms underlying the resolution of evolutionary conflicts. The general outcome of this is that in most taxa where parents provide care females are the primary carer. When males provide care alone they can be as effective as females in caring and increasing offspring survival. In contrast, comparative analyses show that biparental care mainly arises from males joining females and that the main benefit of male (biparental) care is an increase in the productivity of females, not the survival of offspring. The evolution of parental care is a dynamic, multivariate process that involves the co-evolution of multiple traits in males, females and offspring.

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Introduction
Care is complex
One of our children recently defined parental care for us as 'it's complicated and rare, but I know it when I see it.'

Though facetious, this is a reasonable description of the current state of the field. But why should this be so? Part of the problem is that defining care can be difficult — parental care is perhaps better considered a concept than a phenotype that is easily measured — and can take many forms from simple protection of eggs to highly elaborate delivery of food, protection, and housing for developing young [1]. Another problem is there are few universal generalisations, although the exceptions should be informative. Females are more frequently the caregivers when there is care [2], and when males care it is usually with a female partner (i.e., biparental care). Male only care is rare — except in fish where it is the norm for some groups. Even this attempt at generalization is too simple. Not only does the form of care vary taxonomically, there are species where female only care, biparental care and male only care can all be expressed. In some plovers, for example, there is everything from no care (where the nest typically fails) to male only to female only to biparental care, depending on which sex deserts or does not desert the nest [3]. If care is important and beneficial, why is there so much variation? In recognition of this variability, there is increasing realization that parental care is highly complex, both in the terms of the characteristics and behaviours expressed and the factors underlying the evolution of those traits. Observed patterns of parental care, therefore, have not evolved as a single evolutionary transition. Instead, parental care involves the evolution of multiple behaviours that co-evolve in response to and along with many other aspects of the reproductive biology and ecology of a species. Despite the potential difficulties of unravelling this rich complexity, recent studies have provided significant new insights into both the origins and subsequent evolution and diversification of parental care. Here we highlight some of these studies and provide some pointers for future work.

The evolutionary origins of parental care
Ecological factors can increase offspring need and select for care
The first step in the evolution of parental care is a transition from an ancestral state of no care to the existence of some form of parental care. The key factor driving this transition is high offspring need [4,5]. Offspring need is expected to be dictated by extreme environments, either favourable (e.g., rich but ephemeral resources) or unfavourable (e.g., high levels of environmental stress or predation) [6]. In these circumstances parental care is more likely to evolve because offspring survival is low in the absence of care [4,7]. Empirical evidence in support of this idea has been

difficult to come by, largely because there are few species where transitions between states of care from no care have been observed and due to the subsequent evolution of many traits following the origin of care. However, a recent study on long-tailed skinks *Eutropis longicaudata* is an exception [8•]. This species does not normally provide parental care, but maternal care has been observed in one island population. A common garden experiment showed that there was heritable variation underlying the expression of parental care. Field experiments further showed that parental care significantly increased egg survival by reducing the probability of predation by egg-eating snakes (which are not abundant in other populations of skink). A reduction in egg survival as a result of predation by snakes has apparently favoured the evolution of parental care from a non-caring state in this species [8•].

But only if there are appropriate behavioural precursors
Ecological drivers favouring the origin of care alone is too simplistic, as there are alternative solutions to environmental extremes. It has long been recognized parental care only evolves as the solution if there are appropriate behavioural precursors [9]. A recent study by Cunningham *et al.* [10•] on *Nicrophorus vespilloides* burying beetles, which have extended parental care, including offspring provisioning by regurgitation of food to begging larvae [11,12], provides an example of such a precursor. The authors found that gene expression of a pathway that influences motivation to eat is altered during parental care. Specifically the neuropeptide F receptor was down-regulated during active care. This indicates that the provisioning of offspring has evolved via selection acting on, and modifying, self-feeding behaviour [10•].

Once care has originated transgenerational, co-evolutionary effects determine trajectories
Whilst such behavioural precursors provide the necessary kick-start in the right direction co-evolutionary feedback loops are likely to be important in determining subsequent evolutionary trajectories [13,14]. One of the peculiarities of parental care is that it affects both parental and offspring fitness. If heritable, both the care and the effects of care can be genetically correlated, resulting in unexpected influences on the outcome. For example, negative genetic correlations between care and effects of care result in high provisioning mothers having offspring that respond less strongly to provisioning [15]. These correlations can also influence care across generations. A study of earwigs *Forficula auricularia* by Thesing *et al.* [16•] demonstrated that offspring reared without a mother were poorer mothers themselves, and there was a heritable component to this, highlighting the importance of such transgenerational, co-evolutionary effects in the maintenance of parental care once it has originated.

Female care or male care?
Adult mortality rates are important determinants of which sex cares
In both earwigs and long-tailed skinks it is females who provide the care, and not males. Maternal care is most common across the majority of taxa where care exists, including mammals and reptiles [17] and invertebrates [18,19]. However, male care is just as common as female care in amphibians [17] and is more common in fishes than female care [17,20]. In species that can have both female-only and male-only parental care, such as the burying beetle species *Nicrophorus vespilloides* (which also has biparental care), male-only care can be just as effective as female-only care in terms of offspring fitness [21,22], and a recent transcriptomics study showed that gene expression profiles of males caring for young by themselves were very similar to that of females caring by themselves, indicating that male-only care is physiologically and functionally similar to female-only care (Figure 1) [23••]. So what determines whether it is female or male care that evolves from a state of no care? There appears to be no one-size-fits-all answer to this question, and some taxonomic patterns are easier to explain than others. Recent theory indicates that sex differences in initial gamete investment do not explain the origins of these patterns of care. Rather it is relative adult mortality rates that can drive which sex cares [24]: the sex with the higher mortality, that is, reduced future reproductive potential, is the sex more likely to provide care. This is an area where more data would be particularly welcome.

## The evolution of biparental care
Adult sex ratios and the intensity of sexual selection affect the probability of biparental care
Adult mortality rates have also been shown to be important in the evolution of biparental care. Biparental care is a relatively rare form of care in invertebrates [19,21], fishes and mammals [17], but is more common in amphibians, and is the predominant form in birds [17]. Remeš *et al.* [25•] conducted a comparative analysis of 659 species of bird from 113 families that have biparental or uniparental care and found that biparental was less likely as the intensity of sexual selection increased and as adult sex ratios became more skewed, independent of non-social environmental factors such as climate. Adult sex-ratios vary with sex differences in mortality, amongst other things, and sexual selection and parental care both have mortality consequences, so are linked in eco-evolutionary feedback loops [26]. Such sex differences in mortality affect the costs and benefits of care in males and females [24], which can reinforce sex roles in parental care as a result of the co-evolution of care and the ability to provide care [27].

In species with biparental care, males are not as committed to care as females
Because males and females can experience different costs and benefits of care, biparental perhaps more often

Figure 1
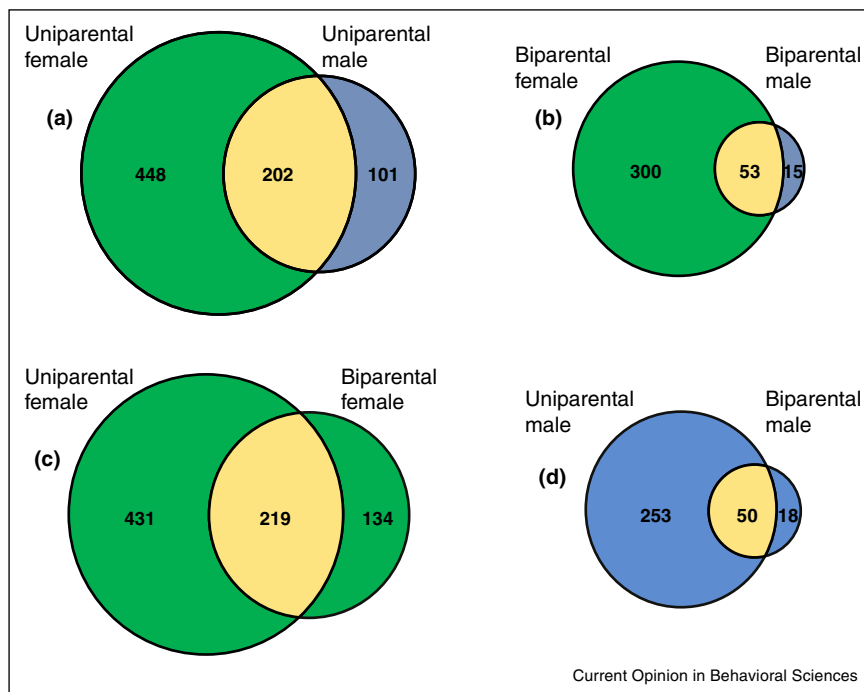
Genetic evidence for reduced participation in biparental care by males. There are few overlapping gene expression changes when comparing biparental males with any other social condition. The pie charts illustrate differential gene expression (in the same direction) in **(a)** caring uniparental females and males, **(b)** caring biparental females and biparental males, **(c)** caring uniparental and biparental females, and **(d)** uniparental and biparental males from before care to during care. Numbers indicate the number of significantly differentially expressed genes, with expression changes in the same direction, in a given social condition (green = female, blue = male, yellow = overlap). Modified from Ref. [23].

describes the social condition of families rather than the combined behavioural contributions of parents in isolation from one another [23••]. Comparative studies across different taxa indicate that biparental care primarily arises from males joining caring females as a result of social environmental factors related to the availability of additional mating opportunities and the ability of males to secure them [19,25•,28,29•]. In the majority of species with biparental care females still provide more care than males [2], and the benefits of male care to offspring success appear to be limited in many species where males care with females, including humans [30,31•]. For example, empirical work on *Nicrophorus vespilloides* burying beetles showed that males spent more time providing care when there was more, not less, male–male competition [32]. Males were therefore primarily 'providing care' to protect their paternity rather than increase offspring survival [32,33]. This is further supported by the transcriptomic study of Parker *et al.* [23••] who found that biparental male gene expression was more similar to non-caring males than to caring females or uniparental males (Figure 1). Consequently males are generally not as committed to care as females in biparental unions, providing plenty of scope for sexual conflict.

## The resolution of sexual conflict
Brood size may co-evolve with male care and resolve sexual conflict

Care is costly and sex differences in these costs leads to selection pressures differing between males and females and thus sexual conflict [34]. So how is the sexual conflict resolved so that biparental care can occur? Stockley & Hobson [29•] tested whether biparental care in mammals, which is rare, evolved because male care improved offspring survival, or, instead, increased offspring productivity (litter size). The results supported the latter indicating that male care co-evolved with litter size when males provision offspring — an increase in male care, perhaps related to paternity protection [32], allowed females to produce larger litters, and the greater the number of offspring the greater the value of male care — stabilizing biparental care and monogamy (Figure 2) [35]. This most likely occurred because female reproductive investment is constrained by life-history trade-offs, but male care relaxes these constraints, allowing females to invest in offspring productivity [29•].

Maternal effects may facilitate conflict resolution

A recent review highlighted how females may facilitate such co-evolution, and resolve sexual conflict, by using
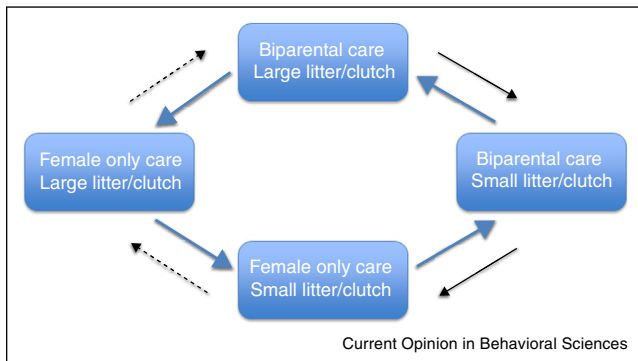
Co-evolution between male (biparental) care and litter/clutch size. In mammals evidence presented in Ref. [29] supported a co-evolutionary pathway whereby litter size increased following the evolution of males joining females to provide care (provisioning), as shown by the blue arrows. The alternative pathway, in the reverse direction was not supported (black arrows). The thickness of the arrows shows the strength of the support for the direction of the transition between states, with dashes indicting particularly weak support. The ancestral state in mammals is female only care with small litter sizes. Male care therefore facilitates an increase in female productivity (see main text for further details). However, in other taxa with biparental care the co-evolutionary pathways are currently unknown. Re-drawn from Ref. [29].

maternal effects as an incentive to males to provide more care [36]. Clutch or litter size can be considered to be a maternal effect because it can have a causal effect on offspring phenotype/fitness [37,38]. The co-evolution of litter size and male care in mammals described by Stockley & Hobson [29•] provides a potential example of this: females may increase litter size in order to 'incentivise' males to stick around longer and increase investment, making the current brood more valuable to the male and male care more valuable to the female [35,38,39], especially if further mating opportunities [40] and/or future reproductive potential [24] are low for males.

Females may use hormones to influence male behaviour and resolve conflict

An insight into the mechanistic basis by which sexual conflict may be resolved and male care encouraged by females in a species with biparental care is illustrated by a new study by Engel *et al.* [41••]. *Nicrophorus vespilloides* burying beetles communicate their hormonal status to their male partners using an anti-aphrodisiac pheromone, methyl geranate. This stops males trying to mate with females whilst they are providing care. Mating at a high frequency is potentially good for males as it provides paternity assurance [42], especially when there is competition from rivals [32], but it is costly for females [43]. Methyl geranate emission is closely linked to production of juvenile hormone, and both peak during offspring provisioning [41••]. Production of methyl geranate during periods of peak care by females signals their temporary
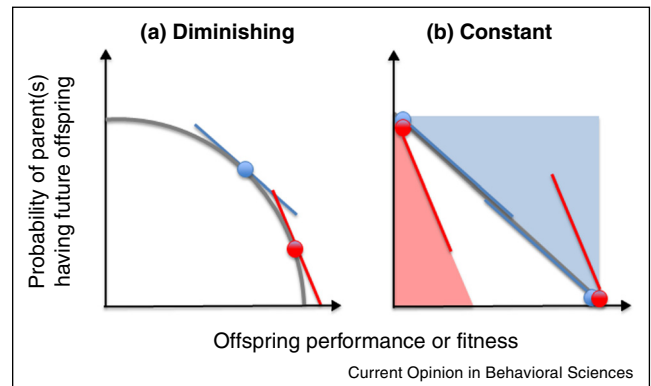
Plots illustrating how the shape of genetic trade-offs affects the battleground of parent-offspring conflict. **(a)** Curved trade-off between the probability of parental future reproduction with current offspring fitness, showing with diminishing returns (grey line). The slope of the fitness tangent for offspring (red line) is steeper (-2) than that of parents (blue line; -1), because offspring are half as related to their (full) siblings as they are to themselves, whereas parents are equally related to all offspring. As a result the optima of parents and offspring differ (blue and red circles, respectively), so there is conflict over the amount of parental investment that should be provided between parents and current offspring. **(b)** Linear trade-off with constant returns. When the parent and offspring slopes are in the blue area there is agreement between parents and current offspring that the parent should not produce future offspring. In contrast, when the parent and offspring slopes are in the red area there is agreement that the parent should terminate current parental care in order to invest in future offspring (i.e., produce another clutch). Only in the white area is there conflict between parent and offspring over whether or not to invest in future offspring. In earwigs, trade-offs were curved with diminishing returns for pre-hatching traits such as egg development rate, but were linear with constant returns for post-hatching traits such as current offspring growth rate and survival probability. Re-drawn from Ref. [45].

infertility to their partners and in doing so switches off the mating drive of males, which may increase the probability he would engage in parental care [44]: hormonal control of male behaviour by females to avoid costly mating helps resolve sexual conflict and may promote the co-evolution of male and female care.

Co-evolution and conflict
Co-evolution can occur without conflict
Does co-evolution of family members always go hand-in-hand with conflict? A study by Kölliker *et al.* [45••] provides significant new insights that suggest not. They used selection lines to test for a genetic conflict between parents and offspring by examining the trade-off between offspring performance and a parent's ability to raise additional offspring in earwigs *Forficula auricularia*. By selecting on female future reproduction (second clutch size) and assessing correlated responses in the survival, development rate and growth of current offspring they established that there were genetic trade-offs between

offspring performance and parental future reproduction. However, the shape of these trade-offs differed before and after hatching: there was evidence that parental investment fitness optima differed between parents and offspring before, and hence there was parent-offspring conflict, but not after, hatching (Figure 3). Parent-offspring conflict is therefore not inevitable and depends upon the shape of the trade-off at different life stages and the specific traits involved. Consequently although there is antagonistic parent-offspring co-evolution parental investment may evolve without conflict in earwigs [45••].

Summary and conclusion

Parental care is complex but recent work is providing significant new insights that are helping to unpack that complexity to reveal some underlying patterns. For example, it is important to recognize that origin is not equivalent to the maintenance or subsequent elaboration of care (Figure 4). Ecological factors that affect offspring survival, such as the rate of predation, combined with associated behavioural precursors and the necessary genetic (co-)variation in behaviour between parents and offspring are central to the origin of parental care (Figure 4a). In contrast, once parental care has originated whether it is maintained or not depends more on adult than offspring mortality, with the benefits of parental care increasing as adult mortality decreases and as the juvenile period increases [7]. Furthermore, co-evolutionary feedback between parents and offspring increases the mutual dependence [46], making it difficult to lose complex care once it has originated [47]. Who, how much and what form of care is provided depends on a suite of inter-related factors

Figure 4
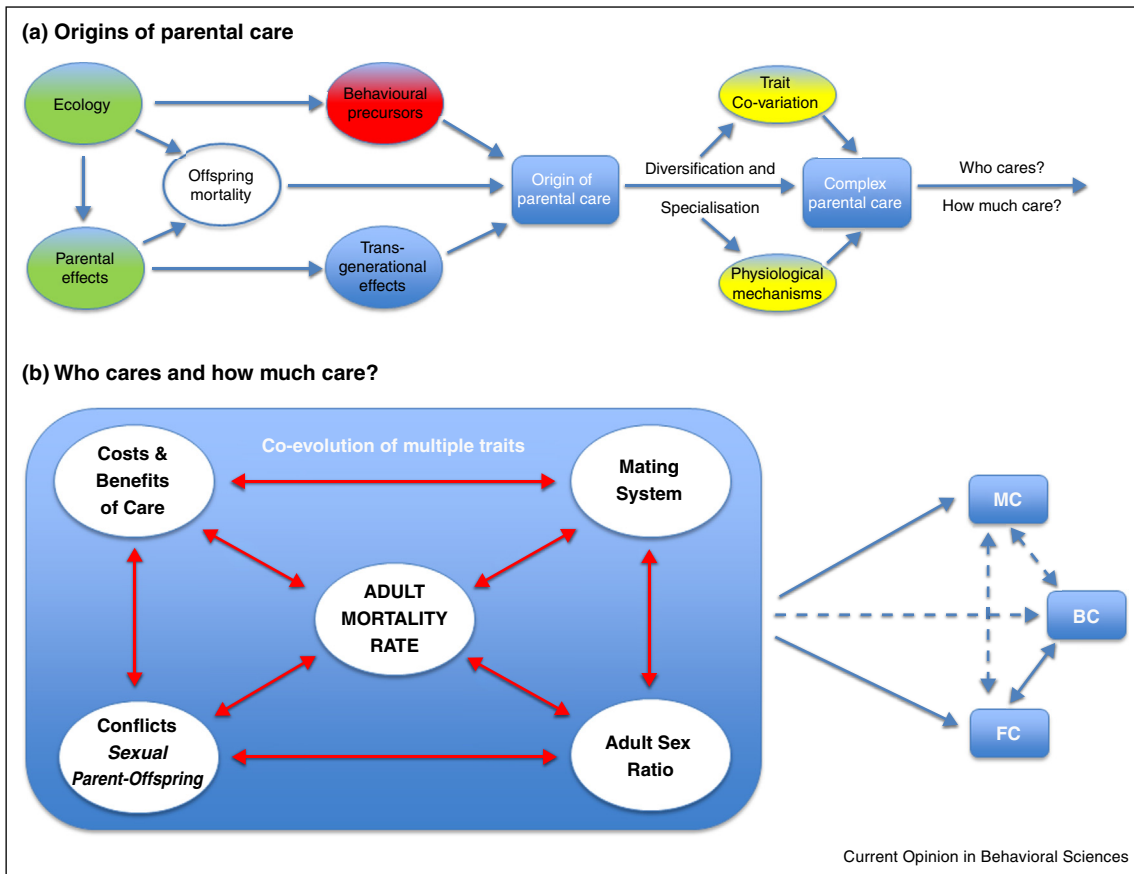
(a) The evolutionary origins of parental care are influenced by a number of factors including ecological (e.g., resource availability, risk of predation) and parental effects (e.g., egg size) that impact patterns of offspring mortality, and therefore, offspring need. However, whether parental care arises is also dependent on the presence of suitable behavioural precursors, and transgenerational effects, such as genetic correlations between parents and offspring, that promote parental behaviours. More complex parental care evolves as a result of co-evolutionary feedback loops involving physiological and cognitive mechanisms that facilitate effective parental care, and the co-variation of traits in parents and offspring. (b) Which parent provides care and how much care they provide depends upon the co-evolution of multiple traits driven by a suite of interrelated factors including adult mortality rate, the costs and benefits of care for males and females, conflicts of interest among family members, the mating system and intensity of sexual selection, and the adult sex ratio. In the majority of taxa with care female only care (FC) predominates, but male only care (MC) is also prevalent in some taxonomic groups (e.g., amphibians and some fishes). Biparental care (BP) predominately arises from female only care. Less frequent transitions in care are shown by the dashed arrows. See main text for further details.

including adult mortality rate [5], parentage and the intensity of sexual selection [2,26], the costs and benefits of care [27], the mechanisms underlying care behaviours and the resolution of conflicts, that affect the co-evolution of multiple traits in family members (Figure 4b). Thus, the complexity of care, involving diverse behaviours (defence, food acquisition and maintenance, nest maintenance, regurgitated food, etc.), may evolve in stepwise fashion. 'Parental care' is therefore multivariate and increases in complexity over time and the nature of this complexity will reflect a variety of factors.

The studies highlighted in this review demonstrate that we need to take a holistic approach that recognizes that parental care is a co-evolving game for the whole family, and even non-caring members of the family may have important effects on the evolution of family life. For example, in the Engel *et al.* [41••] study it is offspring behaviour that likely modifies the production of juvenile hormone during provisioning, and, therefore the anti-aphrodisiac methyl geranate. As a result the more demanding offspring are of their mother the less amorous their father is likely to be: offspring effectively control the mating behaviour of their father via their mother [44]! In another example, caring male sticklebacks *Gasterosteus aculeatus* were less attracted to females that had been stressed by exposure to predators and reduced their subsequent parental care accordingly [48•]. The experiences of the non-caring parent (females) therefore impacted offspring directly via the effects of stress on offspring phenotype, and indirectly, through reduced care by males. Understanding the evolution of parental care requires a dynamic, multivariate [26,46], multidimensional [41••] perspective in combination with use of suites of complimentary tools and approaches. Moreover, it is important to differentiate between studies aimed at explaining the origins versus the elaboration of care. The studies presented here light the way.

Conflict of interest statement
Nothing declared.

Acknowledgements

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