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Evolution of paternal care in diploid and haplodiploid populations

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Abstract

W. D. Hamilton famously suggested that the inflated relatedness of full sisters under haplodiploidy explains why all workers in the social hymenoptera are female. This suggestion has not stood up to further theoretical scrutiny and is not empirically supported. Rather, it appears that altruistic sib-rearing in the social hymenoptera is performed exclusively by females because this behaviour has its origins in parental care, which was performed exclusively by females in the ancestors of this insect group. However, haplodiploidy might still explain the sex of workers if this mode of inheritance has itself been responsible for the rarity of paternal care in this group. Here, we perform a theoretical kin selection analysis to investigate the evolution of paternal care in diploid and haplodiploid populations. We find that haplodiploidy may either inhibit or promote paternal care depending on model assumptions, but that under the most plausible scenarios it promotes – rather than inhibits – paternal care. Our analysis casts further doubt upon there being a causal link between haplodiploidy and eusociality.

Introduction

W. D. Hamilton (1964, 1972) famously suggested that the inflated genetic relatedness of full sisters under haplodiploidy (life-for-life $r = 3/4$) explains why females, and not males, engage in altruistic sib-rearing in hymenopteran societies. This haplodiploidy hypothesis has fallen out of favour with the realization that the average value of siblings of both sexes is exactly the same ($r = 1/2$) for females and males, irrespective of the sex ratio (Charlesworth, 1978; Charnov, 1978; Craig, 1979; Bourke & Franks, 1995; Ross *et al.*, 2013). Rather, it appears that the sex bias in altruistic sib-rearing within this group of insects owes to a sex bias in the provision of parental care among their solitary ancestors, a pattern which holds across other eusocial species in which the original function of workers was nursing (Ross *et al.*, 2013). That is, although their altruism is clearly driven by kin selection, hymenopteran workers are female because females were already equipped with the behaviours and morphologies conducive to successful sib-rearing – a possibility that Hamilton (1964) acknowledged.

Nevertheless, haplodiploidy could still explain the sex of workers if it was itself responsible for the ancestral pattern of parental care in this group. One possibility is that haplodiploidy promoted the evolution of maternal care among the ancestors of the social hymenoptera (Wade, 2001; Linksvayer & Wade, 2005), but theoretical analysis suggests that haplodiploidy is more likely to inhibit than promote maternal care, and in many instances will have no effect at all (Gardner, 2012). Alternatively, haplodiploidy might have inhibited the evolution of paternal care, yielding a similar outcome. This possibility has not yet been explored.

Here, we investigate whether haplodiploidy inhibits the evolution of paternal care. Specifically, we consider the evolutionary fate of paternal care genes that incur costs for their male and/or female carriers but provide benefits to their male carriers' offspring, under diploidy vs. haplodiploidy, outbreeding vs. inbreeding, and adding vs. averaging of gene effects. We derive analytical results using kin selection methodology (Hamilton, 1964; Taylor & Frank, 1996), and we confirm these results with numerical simulation of an explicit population genetics model. In doing so, we evaluate the possibility that haplodiploidy is responsible for social

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hymenopteran workers being female because it inhibited the evolution of paternal care among their ancestors.

Model and results

Kin selection model

Gardner (2012) considered a kin selection model of the evolution of maternal care in order to evaluate the possibility that haplodiploidy has facilitated eusociality by promoting the evolution of maternal care. We adapt that model to investigate the evolution of paternal care, in order to evaluate the possibility that haplodiploidy has led to an exclusively female worker caste by inhibiting the evolution of paternal care. We assume an infinite population of females and males with diploid or haplodiploid inheritance. We consider the evolution of a paternal care gene, which benefits the offspring of its male carriers while carrying a cost for its female and/or male carriers. These costs could potentially owe to pleiotropic effects of the paternal care gene, rather than simply the cost of the behaviour itself. Behavioural genes with pleiotropic effects have been described in nature; for example, genetic variation in the vertebrate melanocortin system has pleiotropic effects on coloration and behaviour in both sexes (Ducrest *et al.*, 2008), and parental care behaviours in burying beetles show positive genetic correlations between sexes (Walling *et al.*, 2008). Accordingly, the fitness of a female is $w_f(G, G')$ and the fitness of a male is $w_m(G, G')$, where G is the individual's breeding value for the paternal care gene and G' is the individual's father's breeding value. We denote by $C_f = -\partial w_f/\partial G$ and $C_m = -\partial w_m/\partial G$ the direct cost of the paternal care gene for females and males, respectively, and we denote by $B_f = \partial w_f/\partial G'$ and $B_m = \partial w_m/\partial G'$ the indirect benefit for female and male offspring of male carriers of the paternal care gene, respectively. We assume that breeding values are determined either through adding or averaging of gene effects. For diploids, $G = g_1 + g_2$ under adding, where g_1 and g_2 are the individual's two genic values, and $G = (g_1 + g_2)/2$ under averaging. For haploids, $G = g$, where g is the individual's single genic value, irrespective of whether gene effects add or average together (see Gardner, 2012 for more discussion of adding vs. averaging of gene effects).

Adding gene effects

Under the assumption that gene effects add together, we find that natural selection favours paternal care under diploidy when

$$-(2+2f)C_f + (1+3f)B_f - (2+2f)C_m + (1+3f)B_m > 0, \quad (1)$$

where f is the coefficient of inbreeding (see Appendix for derivation). The corresponding condition for haplodiploidy is

$$-(2+2f)C_f + (1+f)B_f - C_m + fB_m > 0. \quad (2)$$

Adopting some simplifying assumptions, conditions (1) and (2) can be rearranged into the form $C/B < A$, where A describes the 'potential for paternal care' (*cf.* Gardner, 2012). A relatively high potential means that paternal care is favoured by natural selection even if there is a relatively high cost/benefit ratio, whereas a relatively low potential means that paternal care is disfavoured by natural selection unless the cost/benefit ratio is correspondingly low. In particular, we assume that: (i) the benefit of paternal care accrues equally to a caring father's sons and daughters ($B_f = B_m = B$); (ii) the benefit is positive ($B > 0$); and (iii) one of three scenarios applies regarding the cost of paternal care, namely, that females and males bear the cost of paternal care equally ($C_f = C_m = C$), only females bear the cost of paternal care ($C_f = C$, $C_m = 0$), or only males bear the cost of paternal care ($C_f = 0$, $C_m = C$). The corresponding potentials for paternal care under the adding model of gene effects are given in Table 1 and illustrated in Fig. 1 panels a–c. These analytical results are confirmed by numerical simulation of an explicit population genetics model (Fig. S1; see Appendix for details).

Under full outbreeding ($f = 0$), haplodiploidy either inhibits the evolution of paternal care or has no effect. Specifically, if both sexes bear the cost of paternal care, then the potential for paternal care is $A = 1/2$ under diploidy and $A = 1/3$ under haplodiploidy (Fig. 1 panel a); if only females bear the cost of paternal care, then the potential for paternal care is $A = 1$ under diploidy and $A = 1/2$ under haplodiploidy (Fig. 1 panel b); and if only males bear the cost of paternal care, then the potential for paternal care is $A = 1$ under both diploidy and haplodiploidy (Fig. 1 panel c). Conversely, under full inbreeding ($f = 1$), haplodiploidy may promote or inhibit the evolution of paternal care. Specifically, if both sexes bear the cost of paternal care, then the

Table 1 Potential for paternal care (A, such that the condition for natural selection to favour paternal care is $C/B < A$) as a function of genetic architecture, ploidy, sex-specific effects, and the coefficient of inbreeding (f).

	Potential for paternal care		
Genetic system	Direct cost accrues to both sexes	Direct cost accrues to females only	Direct cost accrues to males only
Gene effects add			
Diploidy	(1+3*f*)/(2+2*f*)	(1+3*f*)/(1+*f*)	(1+3*f*)/(1+*f*)
Haplodiploidy	(1+2*f*)/(3+2*f*)	(1+2*f*)/(2+2*f*)	1+2*f*
Gene effects average			
Diploidy	(1+3*f*)/(2+2*f*)	(1+3*f*)/(1+*f*)	(1+3*f*)/(1+*f*)
Haplodiploidy	(1+2*f*)/(2+*f*)	(1+2*f*)/(1+*f*)	1+2*f*

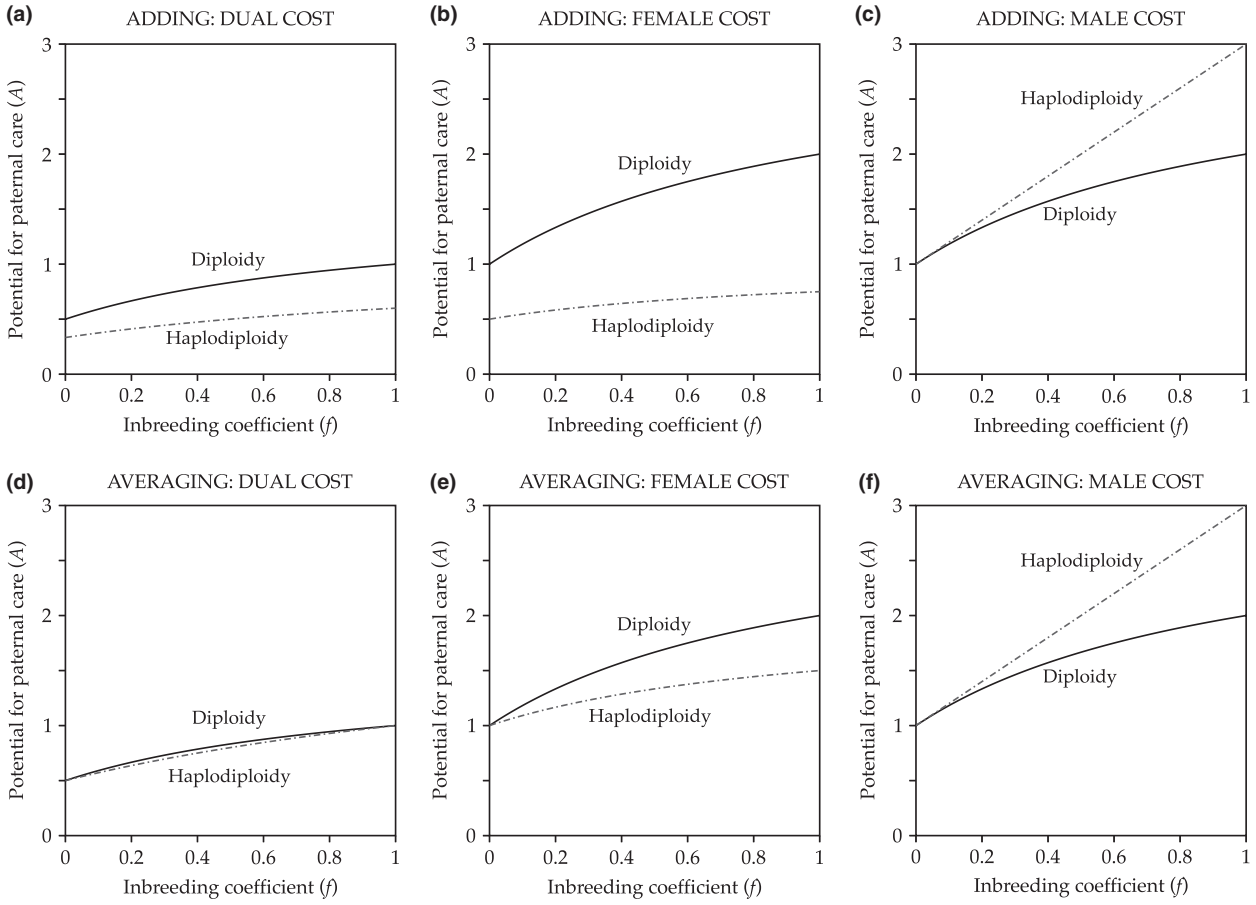

Fig. 1 Potential for paternal care under diploidy vs. haplodiploidy. Analytical solutions for the potential for paternal care (A, such that the condition for natural selection to favour paternal care is $C/B < A$) under diploidy (solid black lines) vs. haplodiploidy (dashed grey lines). Results are shown for: adding of gene effects, with costs experienced by (a) both sexes equally ($C_f = C_m = C$), (b) females only ($C_f = C$, $C_m = 0$) or (c) males only ($C_f = 0$, $C_m = C$); and averaging of gene effects, with costs experienced by (d) both sexes equally ($C_f = C_m = C$), (e) females only ($C_f = C$, $C_m = 0$) or (f) males only ($C_f = 0$, $C_m = C$).

potential for paternal care is $A = 1$ under diploidy and $A = 3/5$ under haplodiploidy (Fig. 1 panel a); if only females bear the cost of paternal care, then the potential for paternal care is $A = 2$ under diploidy and $A = 3/4$ under haplodiploidy (Fig. 1 panel b); and if only males bear the cost of paternal care, then the potential for paternal care is $A = 2$ under diploidy and $A = 3$ under haplodiploidy (Fig. 1 panel c). Intermediate rates of inbreeding ($0 < f < 1$) yield intermediate results (Fig. 1 panels a–c).

Averaging gene effects

Under the assumption that gene effects average together, the condition for natural selection to favour paternal care under diploidy is

$$-(2+2f)C_f + (1+3f)B_f - (2+2f)C_m + (1+3f)B_m > 0. \quad (3)$$

Note that condition (3) is identical to condition (1). The corresponding condition for haplodiploidy is

$$-(1+f)C_f + (1+f)B_f - Cm + fB_m > 0. \quad (4)$$

Following the procedure outlined in the previous section, conditions (3) and (4) can also be rearranged into the form $C/B < A$, where A describes the potential for paternal care. The corresponding potentials for paternal care under the averaging model of gene effects are given in Table 1 and illustrated in Fig. 1 panels d–f; these analytical results are confirmed by numerical simulation (Fig. S1).

Under full outbreeding ($f = 0$), haplodiploidy has no effect upon the evolution of paternal care. Specifically, if both sexes bear the cost of paternal care, then the potential for paternal care is $A = 1/2$ under both diploidy and haplodiploidy (Fig. 1 panel d); if only females bear the cost of paternal care, then the potential for

paternal care is $A = 1$ under both diploidy and haplodiploidy (Fig. 1 panel e); and if only males bear the cost of paternal care, then the potential for paternal care is $A = 1$ under both diploidy and haplodiploidy (Fig. 1 panel f). Conversely, under full inbreeding ($f = 1$), haplodiploidy may promote or inhibit or have no effect upon the evolution of paternal care. Specifically, if both sexes bear the cost of paternal care, then the potential for paternal care is $A = 1$ under both diploidy and haplodiploidy (Fig. 1 panel d); if only females bear the cost of paternal care, then the potential for paternal care is $A = 2$ under diploidy and $A = 3/2$ under haplodiploidy (Fig. 1 panel e); and if only males bear the cost of paternal care, then the potential for paternal care is $A = 2$ under diploidy and $A = 3$ under haplodiploidy (Fig. 1 panel f). Intermediate rates of inbreeding ($0 < f < 1$) yield intermediate results (Fig. 1 panels d–f); note that when both sexes bear the cost of paternal care, haplodiploidy inhibits the evolution of paternal care relative to diploidy for intermediate rates of inbreeding (Fig. 1 panel d).

Discussion

It appears that workers are female in the social hymenoptera because their altruistic sib-rearing derives from the maternal care practiced by their solitary ancestors (Lin & Michener, 1972; Alexander, 1974; West-Eberhard, 1975; Evans, 1977; Charlesworth, 1978; Eickwort, 1981; Craig, 1982; Andersson, 1984; Starr, 1985; Bourke & Franks, 1995; Queller & Strassmann, 1998; Ross *et al.*, 2013). Paternal care is rare among solitary hymenoptera, having only been reported in the genus *Trypoxylon* (Hamilton, 1964; West-Eberhard, 1975; Brockmann, 1980), whereas maternal care is widespread throughout this group (Hamilton, 1964; Hölldobler & Wilson, 1990; Alexander *et al.*, 1991). Furthermore, both theory and empirical evidence suggest that the origin of hymenopteran worker behaviour lies in parental care redirected towards siblings (Wheeler, 1928; Kennedy, 1966; Michener, 1969; Wilson, 1971; Hamilton, 1972; Alexander, 1974; West-Eberhard, 1987; Alexander *et al.*, 1991; Bourke & Franks, 1995; Linksvayer & Wade, 2005; Amdam *et al.*, 2006; Boomsma, 2007; Toth *et al.*, 2006; Boomsma *et al.*, 2011). Hence, the absence of male workers among the social hymenoptera reflects an ancestral dearth of paternal care.

Here, we have investigated the possibility that haplodiploidy inhibits the evolution of paternal care, which, if correct, would potentially explain the pattern of parental care among the ancestors of the social hymenoptera, and hence the contemporary sex bias in worker castes. We have found that haplodiploidy may mediate the evolution of paternal care, but that it may have a positive or negative effect or no effect at all, depending upon which individuals experience the costs of paternal care, the degree of inbreeding, and how gene effects combine to determine phenotypes.

Of most biological relevance is the scenario in which the father pays the cost of paternal care. Here, we have found that for outbred populations ($f = 0$), haplodiploidy neither promotes nor inhibits the evolution of paternal care, irrespective of whether gene effects add or average together, because the value that a male places upon his offspring relative to the value that he places upon himself is the same under diploidy and haplodiploidy. Specifically, although a male places less value upon his 'sons' under haplodiploidy (i.e. zero value, because they develop from his partner's unfertilized eggs, and hence are unrelated to him; Hamilton, 1972), he places more value upon his daughters (because the reproductive value of females is greater under haplodiploidy; Hamilton, 1972), and these two effects exactly cancel.

However, for inbred populations ($f > 0$), haplodiploidy promotes the evolution of paternal care, irrespective of whether gene effects add or average together. This is because inbreeding leads a male to be more related to his offspring under haplodiploidy than under diploidy. Specifically, inbreeding increases the consanguinity of father and offspring under both diploidy and haplodiploidy, increasing the absolute value of offspring under both modes of inheritance. But although inbreeding increases the consanguinity of a male to himself under diploidy (because he is inbred), it does not increase the consanguinity of a male to himself under haplodiploidy (because a haploid individual cannot be inbred), such that the absolute value a male places upon himself is increased by inbreeding under diploidy but not under haplodiploidy. The net effect is that, in the context of inbreeding, a male places relatively more value upon his offspring under haplodiploidy than under diploidy, and hence, under inbreeding, haplodiploidy promotes the evolution of paternal care.

Although we have treated the degree of inbreeding as a fixed parameter when assessing the impact of diploidy vs. haplodiploidy upon the evolution of paternal care, it is possible that rates of inbreeding are systematically different for diploid vs. haplodiploid taxa. One possibility is that haplodiploidy promotes inbreeding by purging the recessive deleterious alleles that make inbreeding costly (White, 1945; Suomalainen, 1962; Crozier, 1970; Brückner, 1978; Henter, 2003). As we have found that inbreeding ($f > 0$) tends to accentuate the impact of haplodiploidy, this effect would tend to magnify the differences between diploidy and haplodiploidy in our analysis. Alternatively, for hymenoptera in particular, inbreeding could be relatively inhibited because of costs associated with the production of sterile diploid males in the context of complementary sex determination (Whiting, 1925, 1933; Cook & Crozier, 1995; van Wilgenburg *et al.*, 2006; for an exception, see

Cowan & Stahlhut, 2004). A negative association between haplodiploidy and inbreeding would tend to reduce the differences observed between diploidy and haplodiploidy in our analysis. The relative importance of these two factors has not been systematically studied, but although inbreeding rates vary among both diploids and haplodiploids, haplodiploidy does appear to be overrepresented among chronic inbreeders (Hamilton, 1967; Werren, 1993).

We have also considered two further scenarios, in which both females and males, or only females, pay the cost of paternal care. These particular cost scenarios are included primarily for synthesis with the analyses of Wade (2001) and Gardner (2012). We have found that haplodiploidy may either inhibit or have no impact upon the evolution of paternal care in these scenarios, depending upon the degree of inbreeding and whether gene effects add or average together to determine the phenotype. Conceptualization of these results is complicated because there are two actor classes: males who actually enact the paternal care behaviour, and females who pay (at least part of) the cost. Broadly speaking, haplodiploidy inhibits the evolution of paternal care when females pay a cost because females have greater reproductive value under haplodiploidy and hence the evolutionary impact of this cost is magnified (*cf*. Gardner, 2012).

These results could illuminate the evolutionary trajectories of particular paternal care genes that incur known costs for their female carriers. This might be relevant in a case where morphologies or behaviours enhancing parental care in males are deleterious when expressed in females, and where the genes underlying these traits are not differentially regulated in the two sexes. Such genes may be sexually antagonistic – that is, experiencing opposing selective pressures in females and in males (Lande, 1980; Rice, 1984). Sexually antagonistic genes have been identified in insect populations (e.g. Innocenti & Morrow, 2010). However, the absence of a clear and necessary ecological trade-off underlying sexual antagonism in paternal care traits means that these results may be of limited relevance to the broader question of whether and how haplodiploidy impacts upon the evolution of paternal care.

Thus, if haplodiploidy has a robust impact upon the evolution of paternal care, our analysis suggests that it is in the opposite direction from that required to explain the female bias in parental care among the ancestors of the social hymenoptera. This provides further support for the idea that haplodiploid inheritance is not responsible for the exclusively female worker caste of the social hymenoptera: either directly, as a result of the inflated genetic relatedness of haplodiploid sisters (Charlesworth, 1978; Charnov, 1978; Craig, 1979); or indirectly, by preadapting females and not males for sib-rearing (Gardner, 2012 and the present analysis). Instead, although the ancestral female bias in parental care provides the best explanation for the female bias in altruistic sib-rearing among the social hymenoptera (Ross *et al*., 2013), the relative absence of paternal care in this group mirrors the more general absence of paternal care across the terrestrial animal kingdom, which owes to other fundamental asymmetries between the sexes (Queller, 1997; Kokko & Jennions, 2012).

More generally, the issue of whether haplodiploidy has been an important determinant of the evolution of helping in the social hymenoptera (the evidence suggests that it has not) is distinct from the issue of whether kin selection has played a key role (the evidence overwhelmingly suggests that it has). Ecological factors, such as those concerning which sex or sexes exhibited parental care in the ancestral species, do not provide alternatives to kin selection, but rather modulate the cost and benefit terms appearing in Hamilton's (1963, 1964, 1970) rule.

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Appendix

Kin selection analysis

Here, we perform a kin selection analysis of the model presented in the main text, analogously to the model of maternal care analysed by Gardner (2012). Having defined w_f and w_m in the main text, we write $\bar{w}_\mathrm{f}$ and $\bar{w}_\mathrm{m}$ for the average fitness of females and males, respectively, and $W_\mathrm{f} = w_\mathrm{f}/\bar{w}_\mathrm{f}$ and $W_\mathrm{m} = w_\mathrm{m}/\bar{w}_\mathrm{m}$ for the relative fitness of a female and a male, respectively. As we assume the paternal care gene is vanishingly rare, $\bar{w}_\mathrm{f} = \bar{w}_\mathrm{m}$. The condition for natural selection to favour any trait is $c_\mathrm{f}\ \mathrm{d}W_\mathrm{f}/\mathrm{d}g_\mathrm{f} + c_\mathrm{m}\ \mathrm{d}W_\mathrm{m}/\mathrm{d}g_\mathrm{m} > 0$ (Taylor, 1996; Taylor & Frank, 1996; Frank, 1997, 1998; Taylor *et al.*, 2007); here, c_f and c_m are the class reproductive values of females and males, respectively (Fisher, 1930; Taylor, 1996; Grafen, 2006), and g_f and g_m denote the genic values of random genes picked from a female and a male, respectively.

A gene's value has both direct and indirect impacts on its carrier's fitness. The direct effect follows from the genic value (g_f or g_m) modifying its carrier's breeding value (G_f or G_m), which in turn may be associated with a fitness cost to the gene's carrier. The indirect effect follows from the statistical association, due to heredity, between the gene's value (g_f or g_m) and its carrier's father's breeding value (G'_f or G'_m), which in turn is associated with the father's investment in paternal care, which may yield a fitness benefit for the gene's carrier. Thus, the two actors who may modify a given recipient's fitness are the recipient itself and the recipient's father. From the chain rule, we have $\mathrm{d}W_\mathrm{f}/\mathrm{d}g_\mathrm{f} = (\partial W_\mathrm{f}/\partial G_\mathrm{f}) \times (\mathrm{d}G_\mathrm{f}/\mathrm{d}g_\mathrm{f}) + (\partial W_\mathrm{f}/\partial G'_\mathrm{f}) \times (\mathrm{d}G'_\mathrm{f}/\mathrm{d}g_\mathrm{f})$. Here, $\partial W_\mathrm{f}/\partial G_\mathrm{f} = -C_\mathrm{f}/\bar{w}_\mathrm{f}$; $\mathrm{d}G_\mathrm{f}/\mathrm{d}g_\mathrm{f}$ is equal to $2p_\mathrm{f}$ for adding of gene effects and p_f for averaging of gene effects, where p_f is the consanguinity of a female to herself (Bulmer, 1994); $\partial W_\mathrm{f}/\partial G'_\mathrm{f} = B_\mathrm{f}/\bar{w}_\mathrm{f}$; and $\mathrm{d}G'_\mathrm{f}/\mathrm{d}g_\mathrm{f}$ is equal to $2p_\mathrm{d}$ for adding of gene effects under diploidy and p_d for adding of gene effects under haplodiploidy and averaging of gene effects under diploidy or haplodiploidy, where p_d is the consanguinity of father and daughter. Similarly, $\mathrm{d}W_\mathrm{m}/\mathrm{d}g_\mathrm{m} = (\partial W_\mathrm{m}/\partial G_\mathrm{m}) \times (\mathrm{d}G_\mathrm{m}/\mathrm{d}g_\mathrm{m}) + (\partial W_\mathrm{m}/\partial G'_\mathrm{m}) \times (\mathrm{d}G'_\mathrm{m}/\mathrm{d}g_\mathrm{m})$. Here, $\partial W_\mathrm{f}/\partial G_\mathrm{m} = -C_\mathrm{m}/\bar{w}_\mathrm{m}$; $\mathrm{d}G_\mathrm{m}/\mathrm{d}g_\mathrm{m}$ is equal to $2p_\mathrm{m}$ for adding of gene effects under diploidy and p_m for adding of gene effects under haplodiploidy and averaging of gene effects under diploidy or haplodiploidy, where p_m is the consanguinity of a male to himself; $\partial W_\mathrm{m}/\partial G'_\mathrm{m} = B_\mathrm{m}/\bar{w}_\mathrm{m}$; and $\mathrm{d}G'_\mathrm{m}/\mathrm{d}g_\mathrm{m}$ is equal to $2p_\mathrm{s}$ for adding of gene effects under diploidy and p_s for adding of gene effects under haplodiploidy and averaging of gene effects under diploidy or haplodiploidy, where p_s is the consanguinity of father and son.

Note that: $c_\mathrm{f} = c_\mathrm{m} = 1/2$ under diploidy and $c_\mathrm{f} = 2/3$ and $c_\mathrm{m} = 1/3$ under haplodiploidy, regardless of the sex ratio (Price, 1970; Taylor, 1996); $p_\mathrm{f} = (1 + f)/2$, where $f = \mathrm{d}g_1/\mathrm{d}g_2 = \mathrm{d}g_2/\mathrm{d}g_1$ is the coefficient of inbreeding; $p_d = (1 + 3f)/4$ under diploidy and $p_d = (1 + f)/2$ under haplodiploidy; $p_\mathrm{m} = (1 + f)/2$ under diploidy and $p_\mathrm{m} = 1$ under haplodiploidy; and $p_s = (1 + 3f)/4$ under diploidy and $p_s = f$ under haplodiploidy. Making these substitutions into the condition $c_\mathrm{f}\ \mathrm{d}W_\mathrm{f}/\mathrm{d}g_\mathrm{f} + c_\mathrm{m}\ \mathrm{d}W_\mathrm{m}/\mathrm{d}g_\mathrm{m} > 0$ recovers inequalities (1)–(4) of the main text.

Here, we have framed our kin selection analysis in terms of coefficients of consanguinity and class reproductive values. In the Introduction, we framed the haplodiploidy hypothesis in terms of life-for-life relatedness, which includes both genetic similarity and individual reproductive value in a single quantity. Gardner *et al.* (2012, Appendix A) provide an overview of the connections between consanguinity, life-for-life and regression relatedness, and individual and class reproductive value.

Population genetics analysis

Here, we develop an explicit population genetics model of the evolution of paternal care, analogous to the maternal care model analysed by Gardner (2012).

Diploidy

We assume an infinite population of females and males with genetic variation at a single locus with two alleles, the paternal care allele A and the null allele a. The proportion of females carrying $x \in \{0, 1, 2\}$ copies of A is ϕ_x, and the proportion of males carrying $u \in \{0, 1, 2\}$ copies of A is μ_u. Similarly, we index maternal genotypes by $y \in \{0, 1, 2\}$ and paternal genotypes by $v \in \{0, 1, 2\}$. In the construction of mating pairs, we use the parameter α to control inbreeding. First, females and males are paired preferentially with 'matching' genotypes – AA females with AA males, Aa females with Aa males and aa females with aa males – with any unpaired individuals paired randomly; then, a proportion $1 - \alpha$ of these pairs is broken up and repaired randomly. Therefore, the frequency of x-female/u-male pairs is $\gamma_{xu} = \alpha\ \min(\phi_x,\ \mu_u) + (1 - \alpha)\ \phi_x\mu_u$ if $x = u$, and $\gamma_{xu} = \alpha\ (\phi_x - \min(\phi_x,\ \mu_x))\ (\mu_u - \min(\phi_u,\ \mu_u))/(\Sigma_{z\ \in\ \{0,\ 1,\ 2\}}\ (\mu_z - \min(\phi_z,\ \mu_z))) + (1 - \alpha)\ \phi_x\mu_u$ if $x \neq u$. When genotype frequencies are equal for males and females, the $x \neq u$ case gives $\gamma_{xu} = (1 - \alpha)\ \phi_x\mu_u$. Each pair produces a large number of offspring with an even sex ratio; each offspring's genotype comprises a random allele from the mother and a random allele from the father. Thus, the probability that a daughter born to a y-mother and a v-father is of genotype x is $\pi_{xyv} = \Sigma_{X\ \in\ \{0,\ 1\}}\ \mathscr{B}(X;\ y/2)\ \mathscr{B}(x - X;\ v/2)$, where $\mathscr{B}(q;\ r)$ is equal to r if $q = 1$, $1 - r$ if $q = 0$, and 0 otherwise; and the probability that a son born to a y-mother and a v-father is of genotype u is $\rho_{uyv} = \Sigma_{U\ \in\ \{0,1\}}\ \mathscr{B}(U;\ y/2)\ \mathscr{B}(u - U;\ v/2)$. The total

proportion of x-daughters with a v-father is $\phi_{xv} = \Sigma_y \pi_{xyv} \gamma_{yv}$, and the total proportion of u-sons with a v-father is $\mu_{uv} = \Sigma_y \rho_{uyv}\gamma_{yv}$. Offspring undergo viability selection; the relative proportion of x-daughters with v-fathers who survive to adulthood is $s_{xv} = \beta - C_f \varepsilon_f x + B_f \varepsilon_m v$, and the proportion of u-sons with v-fathers who survive to adulthood is $t_{uv} = \beta - C_m \varepsilon_m u + B_m \varepsilon_m v$, where: β is baseline fitness; C_f, B_f, C_m and B_m are as defined in the main text; and $\varepsilon_f = \varepsilon_m = 1$ under adding of gene effects and $\varepsilon_f = \varepsilon_m = 1/2$ under averaging of gene effects. The average viability for females is $S = \Sigma_{x,v} s_{xv}\phi_{xv}$, and the average viability for males is $T = \Sigma_{u,v} t_{uv}\mu_{uv}$. Finally, an equal number of surviving females and males become the breeders for the next generation, returning the population to the beginning of the cycle with genotype frequencies $\phi'_x = \Sigma_v s_{xv}\phi_{xv}/S$ for females and $\mu'_u = \Sigma_v t_{uv}\mu_{uv}/T$ for males.

Haplodiploidy

We follow the same procedure as above, except for the following changes: male genotypes range over u, $v \in \{0, 1\}$; AA females preferentially pair with A males, aa females preferentially pair with a males, and Aa females have no preference, making the frequency of x-female/u-male breeding pairs $\gamma_{xu} = \alpha \min(\phi_x, \mu_u) + (1 - \alpha)\phi_x\mu_u$ if $x = 2u$, $\gamma_{xu} = \alpha(\mu_u - \min(\phi_{2u}, \mu_u) - (\phi_{2-2u} - \min(\phi_{2-2u}, \mu_u))) + (1 - \alpha)\phi_x\mu_u$ if $x = 1$, and $\gamma_{xu} = \alpha(\phi_{2-2u} - \min(\phi_{2-2u}, \mu_u)) + (1 - \alpha)\phi_x\mu_u$ otherwise; the probability that a daughter born to a genotype-y mother and a genotype-v father is of genotype x is $\pi_{xyv} = \Sigma_{X \in \{0,1\}} \mathscr{B}(X; y/2)\,\mathscr{B}(x\text{-}X; v)$, and the probability that a son born to a genotype-y mother and a genotype-v father is of genotype u is $\rho_{uyv} = \mathscr{B}(u; y/2)$; and $\varepsilon_m = 1$ under both adding and averaging of gene effects.

Inbreeding

To compute the coefficient of inbreeding f in our simulated population, we define a random variable κ according to the presence ($\kappa = 1$) or absence ($\kappa = 0$) of allele A in a random gamete produced by a random female, and a random variable λ according to the presence ($\lambda = 1$) or absence ($\lambda = 0$) of allele A in a random gamete produced by the same female's mate. Then, $f = \mathrm{cov}(\kappa, \lambda)/\mathrm{cov}(\kappa, \kappa)$, where $\mathrm{cov}(\kappa, \lambda) = E(\kappa\lambda) - E(\kappa)E(\lambda) = (\Sigma_{x,u}(xu/4)\gamma_{xu}) - (\Sigma_{x,u}(x/2)\gamma_{xu})(\Sigma_{x,u}(u/2)\gamma_{xu})$ under diploidy and $\mathrm{cov}(\kappa, \lambda) = (\Sigma_{x,u}(xu/2)\gamma_{xu}) - (\Sigma_{x,u}(x/2)\gamma_{xu})(\Sigma_{x,u}u\gamma_{xu})$ under haplodiploidy, and $\mathrm{cov}(\kappa, \kappa) = \mathrm{E}(\kappa^2) - \mathrm{E}(\kappa)^2 = (\Sigma_{x,u}(x/2)\gamma_{xu}) - (\Sigma_{x,u}(x/2)\gamma_{xu})^2$ under both diploidy and haplodiploidy (Gardner, 2012). We use the parameter α to control the amount of inbreeding during the construction of mating pairs; for an inbreeding population at equilibrium under neutrality, $f = \alpha/(2 - \alpha)$. This follows because under neutrality, allele frequencies are the same in both sexes, and so $\mathrm{E}(\kappa\lambda) - \mathrm{E}(\kappa)\mathrm{E}(\lambda) = [\alpha(\phi_1/4 + \phi_2) + (1 - \alpha)p^2] - p^2$ and $\mathrm{E}(\kappa^2) - \mathrm{E}(\kappa)^2 = p - p^2$, where $\phi_2 = p^2 + fpq$ and $\phi_1 = 2pq(1 - f)$ (Wright, 1921; Li, 1955), p is the frequency of allele A, and $q = 1 - p$.

Numerical simulations

We initialize genotype frequencies to $\phi_0 = \mu_0 = 0.999$, $\phi_1 = \mu_1 = 0.001$, and $\phi_2 = \mu_2 = 0.000$ under diploidy and $\phi_0 = 0.999$, $\phi_1 = 0.001$, $\phi_2 = 0.000$, $\mu_0 = 0.9995$, and $\mu_1 = 0.0005$ under haplodiploidy. For viability selection, we assume that $\beta = 1$ and $C = 0.001$. We then perform the above numerical recursions for ϕ_x and μ_u, allowing 100 generations to pass with the paternal care gene 'switched off' (i.e. setting $C_f = C_m = B_f = B_m = 0$). Then, we record the coefficient of relatedness f and the frequency of the paternal care gene (i.e. $1/2\,[1/2\,\phi_1 + \phi_2] + 1/2\,[1/2\,\mu_1 + \mu_2]$ for diploidy and $2/3\,[1/2\,\phi_1 + \phi_2] + 1/3\,\mu_1$ for haplodiploidy). We then 'switch on' the paternal care gene, setting C_f, C_m, B_f and B_m to their desired values, and allow another 900 generations to pass. We consider the paternal care gene to have invaded if its frequency after the 900 generations of selection is greater than it was before those 900 generations.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Invasion of a paternal-care allele under diploidy and haplodiploidy.

Data deposited at Dryad: doi:10.5061/dryad.qr0rn

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