

LETTER

The ecology of sex explains patterns of helping in arthropod societies

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Abstract

Across arthropod societies, sib-rearing (*e.g.* nursing or nest defence) may be provided by females, by males or by both sexes. According to Hamilton's 'haplodiploidy hypothesis', this diversity reflects the relatedness consequences of diploid vs. haplodiploid inheritance. However, an alternative 'preadaptation hypothesis' instead emphasises an interplay of ecology and the co-option of ancestral, sexually dimorphic traits for sib-rearing. The preadaptation hypothesis has recently received empirical support, but remains to be formalised. Here, we mathematically model the coevolution of sex-specific helping and sex allocation, contrasting these hypotheses. We find that ploidy *per se* has little effect. Rather, the ecology of sex shapes patterns of helping: sex-specific preadaptation strongly influences who helps; a freely adjustable sex ratio magnifies sex biases and promotes helping; and sib-mating, promiscuity, and reproductive autonomy also modulate the sex and abundance of helpers. An empirical survey reveals that patterns of sex-specific helping in arthropod taxa are consistent with the preadaptation hypothesis.

Keywords

Eusociality, haplodiploidy, inbreeding, inclusive fitness, local mate competition, local resource enhancement, manipulation, preadaptation, sex ratio, sib-mating.

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INTRODUCTION

Arthropod societies are characterised by individuals who, voluntarily or under manipulation, sacrifice their reproductive potential for their siblings' welfare. This 'helping' behaviour – whether it involves nursing juveniles, habitat construction or home defence – is often sex-biased, meaning that either females or males systematically invest more into sib-rearing. A familiar example of sex-biased helping is furnished by the social Hymenoptera (wasps, bees and ants), whose exclusively-female workforce is often contrasted with the mixed-sex workforce of the social cockroaches (termites).

Hamilton's (1964, 1972) 'haplodiploidy hypothesis' invoked the genetics of sex determination to explain this diversity. Hamilton argued that haplodiploid inheritance, as exhibited by the Hymenoptera, promotes female-biased helping because haplodiploid females are more related to sisters (life-for-life $R = 0.75$) than offspring ($R = 0.5$). In contrast, the termites' diploid inheritance does not promote a sex bias, because diploid individuals are equally related to siblings and offspring of either sex ($R = 0.5$). Under this view, inflated sororal relatedness also explains haplodiploids' apparent predisposition for sociality.

But in spite of its elegance, the haplodiploidy hypothesis has not stood up to further theoretical or empirical scrutiny. Crucially, haplodiploid females have comparatively low relatedness to brothers ($R = 0.25$), which exactly balances their high relatedness to sisters. Hence, haplodiploidy's relatedness

asymmetries should neither promote helping overall, nor encourage female helping in particular, compared to diploidy (Trivers & Hare 1976; Craig 1979; Bourke & Franks 1995; Crozier & Pamilo 1996; Boomsma 2007; Gardner *et al.* 2012; Ross *et al.* 2013). Moreover, a broader view of arthropod sociality, beyond the eusocial insects, reveals extensive diversity in the sex of helpers – from all-female to mixed-sex to all-male – that is not readily explained by ploidy (Fig. 1).

Accordingly, an alternative 'preadaptation hypothesis' has been suggested to explain patterns of helping in arthropods. This hypothesis holds that sex-biased helping reflects ancestral sexual dimorphism for traits subsequently co-opted for sib-rearing (Ross *et al.* 2013). For example, female-biased alloparental care is expected where ancestors provided maternal, but not paternal, care (Wheeler 1928; Lin & Michener 1972; Alexander 1974; West-Eberhard 1975; Evans 1977; Charlesworth 1978; Eickwort 1981; Craig 1982; Andersson 1984; Starr 1985; Bourke & Franks 1995; Crozier & Pamilo 1996; Queller & Strassmann 1998; Gardner & Ross 2013). Indeed, this logic explains more variation in helper sex across animal societies than the classic ploidy-centric view (Ross *et al.* 2013).

However, the preadaptation hypothesis has only been verbally articulated, not theoretically formalised. Moreover, the ecology of sex more generally – that is, the structure of the social environment with respect to sexual reproduction – remains little-explored as an evolutionary driver of patterns of arthropod sociality, perhaps owing to the traditional emphasis on ploidy in this clade (Boomsma 2007). For instance, while

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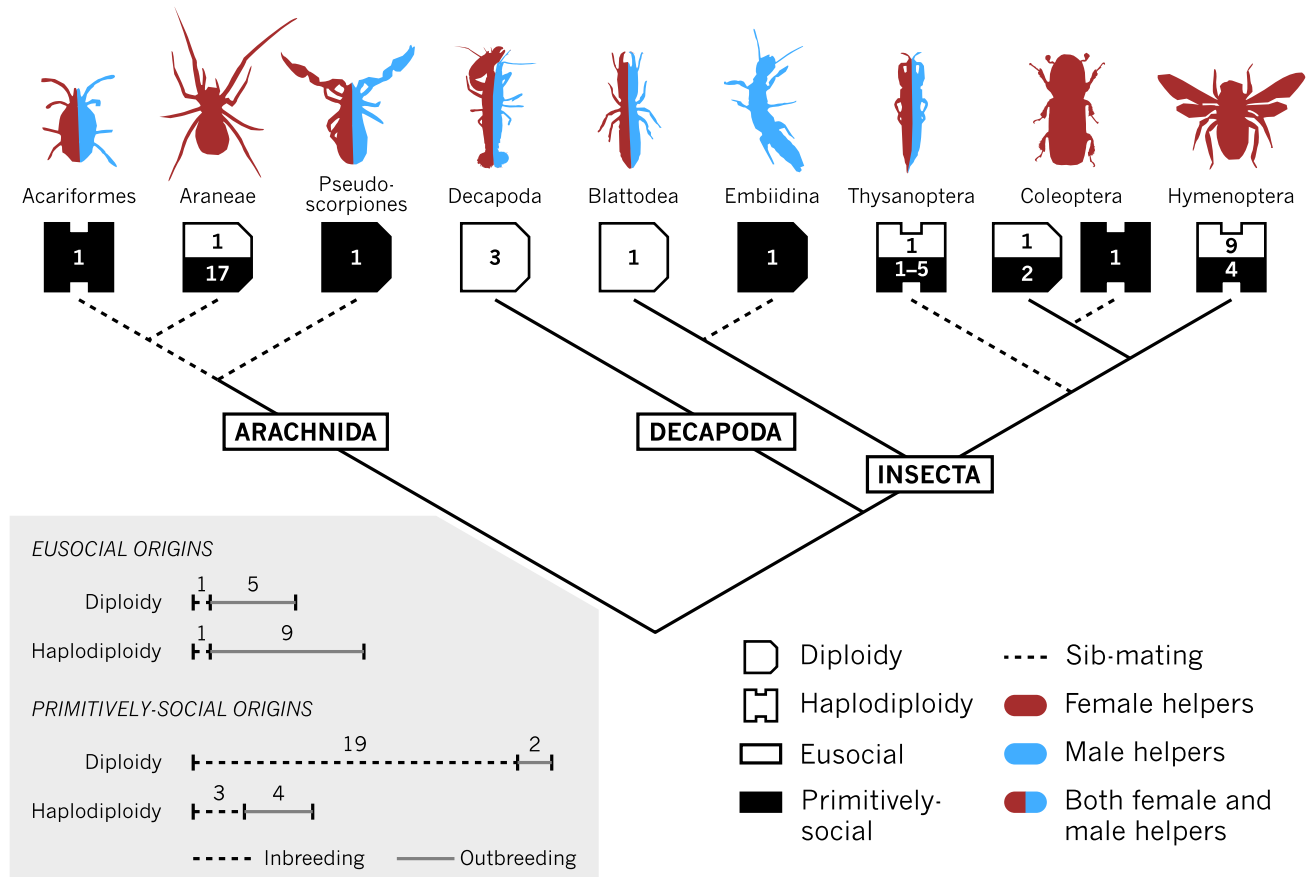


Figure 1 The 44 known independent origins of sib-rearing among eusocial and primitively social arthropods, broken down by ploidy, type of social organisation, presence or absence of sib-mating and sex of helpers. Numbers within tree tips give the number of independent origins of sib-rearing within each taxon. *Inset, lower left*: distribution of origins of eusociality and primitive sociality, for diploidy vs. haplodiploidy and inbreeding (sib-mating) vs. outbreeding taxa. Phylogeny is based on Misof *et al.* (2014).

sex allocation in cooperative-breeding vertebrates is comparatively well-understood (Emlen *et al.* 1986; Pen & Weissing 2000), more recent theory has highlighted a potential for positive feedback between sex-ratio bias and sex-biased helping, particularly in haplodiploid taxa that can readily adjust the sex ratio (Gardner & Ross 2013); yet the implications of such dynamics under sex-specific preadaptation to helping remain obscure. And although inbreeding is prevalent among social arthropods (Fig. 1), and impacts upon relatedness in sex-specific and ploidy-specific ways (Frank 1985; Herre 1985), inbreeding-associated mating ecologies have been largely neglected in relation to the haplodiploidy and preadaptation hypotheses (Bourke & Franks 1995; Crozier & Pamilo 1996).

Here, we develop a mathematical kin-selection model exploring the coevolution of sex allocation and sex-biased helping, under diploidy vs. haplodiploidy and over a range of sexual ecologies: varying sex differences in preadaptation for sib-rearing; fixed vs. evolutionarily labile sex allocation; mating systems spanning full outbreeding to full sib-mating and strict monogamy to extreme promiscuity; and voluntary vs. maternally manipulated helping. This analysis yields quantitative predictions for when we expect helping by females, males or both sexes, and we evaluate these predictions qualitatively

with an empirical comparative survey of all known origins of sib-rearing among arthropods.

MATHEMATICAL ANALYSIS

Life cycle

A mated female produces many offspring on a patch, spending a proportion $1 - z$ of her resources on daughters and z on sons. On average, daughters invest a proportion x , and sons invest a proportion y of their reproductive resources into helping. To simplify interpretation, we assume females and males are equally costly, making z the sex ratio, and assume x and y are propensities for joining a sterile helper caste, although they could represent any costly investment into sib-rearing. Each female helper raises b_f , and each male helper b_m extra siblings; thus, $b_f \neq b_m$ indicates sex-specific preadaptation to sib-rearing. A proportion $1 - s$ of reproductive males disperse, and males from other patches immigrate. Then, mating occurs randomly within patches; consequently, sib-mating occurs with probability s . By default we assume strict monogamy, as this is most empirically relevant (Boomsma 2007, 2009, 2013; Hughes *et al.* 2008), but we also provide results

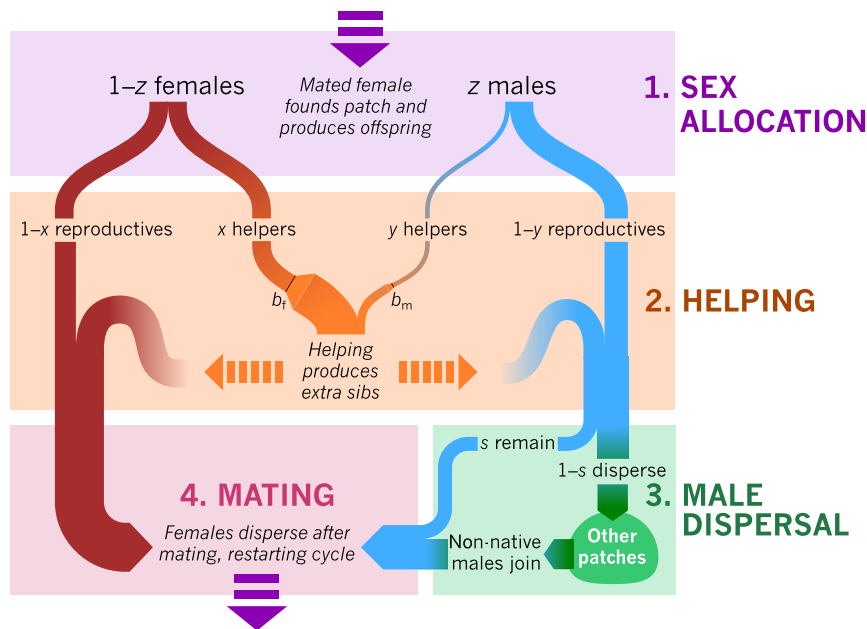


Figure 2 Life cycle used in the model. (1) Sex allocation: the foundress allocates a proportion z of her resources to sons and $1 - z$ to daughters. (2) Helping: daughters invest a proportion x of their resources into sib-rearing, and sons invest a proportion y . The benefit of helping by females and males (b_f and b_m , respectively) determine the number of additional siblings surviving to maturity. (3) Male dispersal: reproductive males stay at home to mate with probability s , otherwise dispersing to other patches, and males from other patches immigrate to the focal patch. (4) Mating: reproductives mate within patches, such that s is the expected probability of sib-mating. After mating, gravid females disperse, founding new patches.

for any degree of promiscuity. After mating, gravid females disperse to found new patches, restarting the cycle (Fig. 2).

Dynamics and statics

Our analysis comprises three methodologies. First, we employ Taylor & Frank's (1996) neighbour-modulated fitness method, a recipient-centred approach to kin selection (Hamilton 1964). This yields analytical conditions for natural selection's effect on sex allocation, female helping and male helping, allowing us to identify stable states for each. Second, we determine these states' reachability by numerically integrating the selection gradients starting from no helping ($x = y = 0$). Third, we assess our analytical results' robustness against a more realistic interplay of selection, mutation, drift and standing genetic variation using stochastic individual-based simulations. (See Supporting Information for full methods and simulation results.)

Sex allocation

Natural selection favours mothers to increase their investment into sons, z , when

$$\underbrace{-p_{\text{dau}} \frac{c_f}{N(1-z)} + p_{\text{son}} \frac{c_m}{Nz}}_{\text{rarer-sex effect}} + \underbrace{(b_m y - b_f x) \left[(1-z) p_{\text{dau}} \frac{c_f}{N(1-z)} + z p_{\text{son}} \frac{c_m}{Nz} \right]}_{\text{local resource enhancement effect}} \\
 + \underbrace{-s p_{\text{son}} \frac{c_m}{N(1-z)} + s^2 p_{\text{son}} \frac{c_m}{Nz}}_{\text{local mate competition effect}} + \underbrace{(b_m y - b_f x) \left[(1-z) s p_{\text{son}} \frac{c_m}{N(1-z)} - z s^2 p_{\text{son}} \frac{c_m}{Nz} \right]}_{\text{local mate enhancement effect}} > 0. \quad (1)$$

To interpret this condition, read the left-hand side as gathering the inclusive-fitness effects experienced by a mother who sacrifices a daughter to produce an extra son. If the sum of these effects is greater than zero, this trade improves the mother's inclusive fitness, so natural selection will favour an increase in z (Fig. 3). Each term in condition 1 is constructed from three measures of value (Frank 1998): a marginal fitness cost or benefit for a recipient; the foundress's consanguinity with the recipient (the probability that randomly picked genes from each are identical by descent; Bulmer 1994); and the recipient's reproductive value (RV), measuring their long-term genetic contribution to the population.

Accordingly, the rarer-sex effect captures the face value of trading away a daughter for a son, ignoring knock-on effects for other relatives. The daughter has consanguinity p_{dau} with her mother, and her RV is $c_f/(N(1-z))$, while the son has consanguinity p_{son} with his mother, and his RV is $c_m/(Nz)$. Here: $p_{\text{dau}} = p_{\text{son}} = 1/(4-3s)$ under diploidy, and $p_{\text{dau}} = 1/(4-3s)$, $p_{\text{son}} = (2-s)/(4-3s)$ under haplodiploidy (see Supporting Information); c_f and c_m are the total RV of females and males, respectively ($c_f = c_m = 1/2$ under diploidy, while $c_f = 2/3$, $c_m = 1/3$ under haplodiploidy); and N is the total population size. For diploids and outbred haplodiploids,

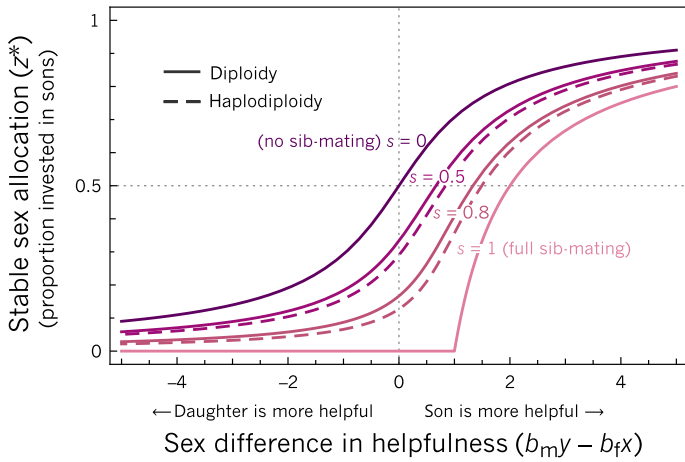


Figure 3 The stable strategy for sex allocation. Mothers are favoured to overproduce individuals of the more helpful sex, according to the sex difference in helpfulness $b_{m,y} - b_{f,x}$ (whether a daughter or a son helps raise more offspring, on average; ordinate axis) and to produce more daughters as the rate of sib-mating, s , increases (darker to lighter lines), a tendency which is exaggerated under haplodiploidy (dashed lines) when sib-mating is intermediate ($0 < s < 1$).

$p_{dau}c_f = p_{son}c_m$, so the rarer-sex effect favours increased investment into sons when $z < 1/2$, but decreased investment into sons when $z > 1/2$, and hence an even sex allocation, $z = 1/2$, overall (Darwin 1871; Düsing 1883; Fisher 1930). But for inbred haplodiploids, $p_{dau}c_f > p_{son}c_m$, and hence inbreeding *per se* increases a mother’s relative valuation of her daughters under haplodiploidy, favouring a relatively female-biased sex ratio (Hamilton 1972; Frank 1985; Herre 1985).

The local resource enhancement (LRE) effect obtains when the sexes differ in helpfulness ($b_{f,x} \neq b_{m,y}$). In trading away a potential female helper for a potential male helper, the mother gains, on average, $b_{m,y} - b_{f,x}$ successfully raised offspring: a proportion $1-z$ of these are daughters, each worth $p_{dau}c_f/(N(1-z))$, and a proportion z are sons, each worth $p_{son}c_m/(Nz)$. The LRE effect favours a relative sex-ratio bias towards the more-helpful sex, increasing the overall investment in helping (Trivers & Willard 1973; Pen & Weissing 2000; Gardner & Ross 2013).

The local mate competition (LMC) effect obtains in the context of sib-mating ($s > 0$). Trading a daughter for a son means one fewer potential mating partner (the daughter) and one more potential mate competitor (the son) for males mating on the patch (Hamilton 1967; Taylor 1981). As male RV comes from mating with females, the daughter’s forfeiture incurs – on average – the loss of a fraction $1/(N(1-z))$ of total male RV for a locally mating male, whose expected consanguinity to the foundress is sp_{son} . Simultaneously, the RV gained by the additional son, $c_m/(Nz)$, entails an equal loss from his mate competitors, who are his brothers to the extent s^2 that neither he nor his brothers disperse before mating, and hence have consanguinity s^2p_{son} to the foundress. These costs of LMC favour a relatively female-biased sex ratio (Hamilton 1967).

Finally, the ‘local mate enhancement’ (LME) effect stems from an interaction between LRE and LMC. Specifically, in trading a daughter for a son, the mother gains $(b_{m,y} - b_{f,x})(1-z)$ daughters and $(b_{m,y} - b_{f,x})z$ sons through

sib-rearing. As above, each daughter yields an inclusive-fitness benefit $sp_{son}c_m/(N(1-z))$ by alleviating LMC, while each son yields an inclusive-fitness cost $-s^2p_{son}c_m/(Nz)$ by intensifying LMC. The net effect of LME is zero when sib-mating is absent ($s = 0$) or complete ($s = 1$), but otherwise ($0 < s < 1$) it slightly favours investment in the more-helpful sex (Fig. S1, Supporting Information).

Sex-specific helping

Voluntary helping – Natural selection favours an increase in voluntary helping by females, x , when

$$\underbrace{-p_{self|f} \frac{c_f}{N(1-z)(1-x)}}_{\text{sacrifice effect}} + \underbrace{b_f \left[(1-z)p_{sis|f} \frac{c_f}{N(1-z)} + zp_{bro|f} \frac{c_m}{Nz} \right]}_{\text{sib-rearing effect}} - \underbrace{sp_{bro|f} \frac{c_m}{N(1-z)(1-x)}}_{\text{LMC effect}} + \underbrace{b_f \left[(1-z)sp_{bro|f} \frac{c_m}{N(1-z)} + zs^2p_{bro|f} \frac{c_m}{Nz} \right]}_{\text{LME effect}} > 0. \tag{2}$$

The left-hand side gathers the inclusive-fitness effects experienced by a reproductive female who joins a sterile helper caste. Analogously to condition 1, the four labelled effects reflect distinct selection pressures which, together, shape female helping (Fig. 4a). Above, $p_{self|f} = (2-s)/(4-3s)$, $p_{sis|f} = p_{bro|f} = 1/(4-3s)$ under diploidy, and $p_{self|f} = (2-s)/(4-3s)$, $p_{sis|f} = (3-s)/(8-6s)$, $p_{bro|f} = 1/(4-3s)$ under haplodiploidy.

The sacrifice effect captures the female’s lost RV – the total female RV divided by the number of reproductive females in the population – weighted by her consanguinity to herself, $p_{self|f}$. All else being equal, as the sex ratio becomes more female-biased, the direct cost of helping decreases, promoting female helping (*cf.* Gardner & Ross 2013). This mirrors the rarer-sex effect (condition 1) in that female reproduction is devalued when females are more abundant.

The sib-rearing effect describes the inclusive-fitness benefit of rearing extra siblings, in the absence of any knock-on effects on mating ecology. Specifically, the female raises $b_f(1-z)$ extra sisters, each worth $p_{sis|f}c_f/(N(1-z))$, and b_fz extra brothers, each worth $p_{bro|f}c_m/(Nz)$. By increasing relatedness, inbreeding ($s > 0$) increases a female’s relative valuation of her siblings, which promotes helping, and this effect is stronger under diploidy than haplodiploidy.

The LMC effect obtains in the context of sib-mating ($s > 0$), such that a female joining the sterile helper caste means one fewer potential mate for her brothers. Specifically, a reproductive female represents, on average, $c_m/(N(1-z)(1-x))$ units of male RV (*cf.* Sex allocation, above), so the female helper incurs this loss for locally mating males, who have expected consanguinity $sp_{bro|f}$ to the female. This cost of LMC inhibits female helping and, indeed, exactly cancels the promoting effect of inbreeding (previous paragraph), under both diploidy and haplodiploidy.

Finally, the LME effect captures an interaction between sib-rearing and LMC. By helping, the female rears $b_f(1-z)$ extra sisters and b_fz extra brothers. Each sister, by alleviating

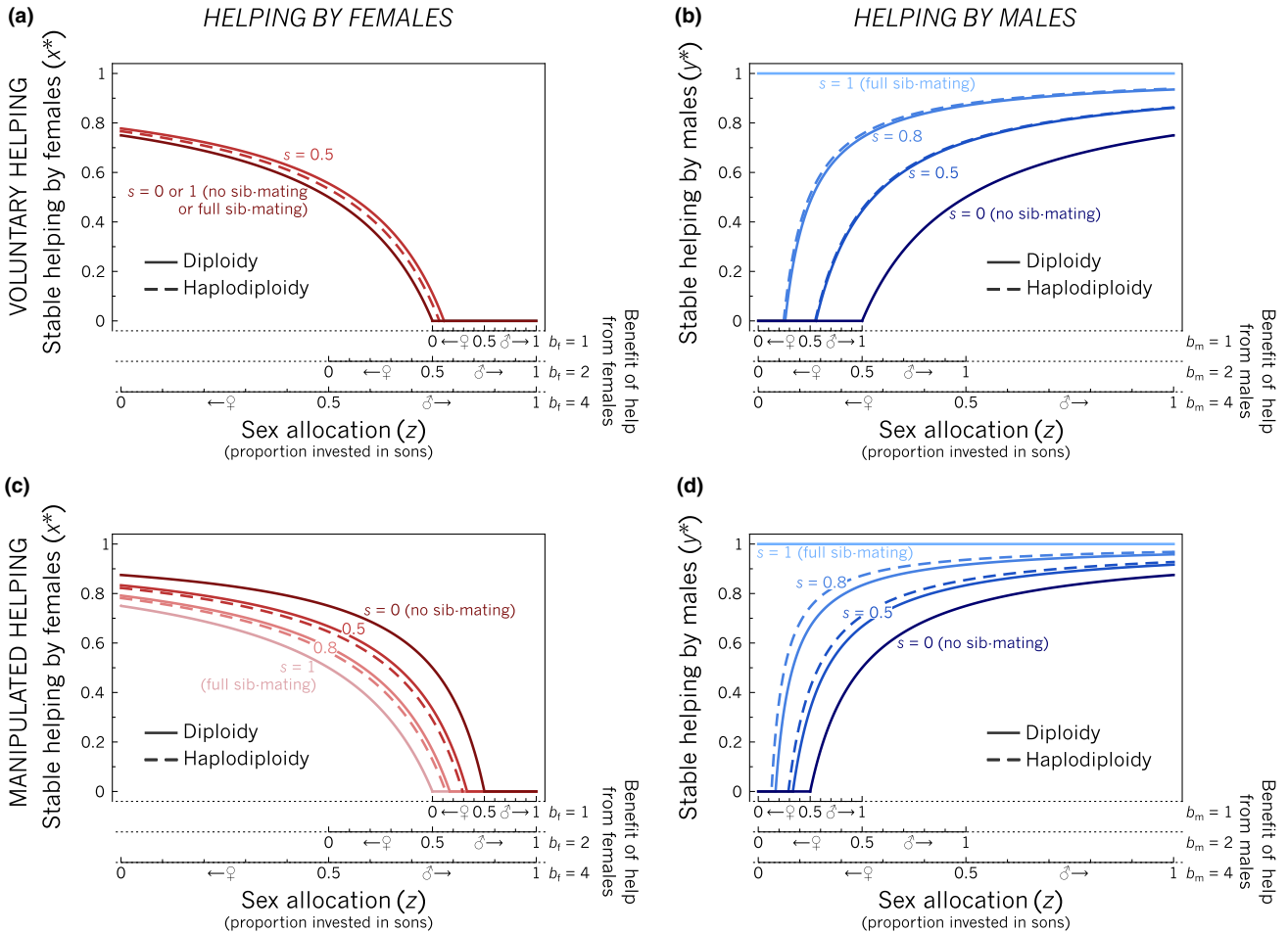


Figure 4 The stable strategy for helping by females and males. Individuals are favoured to help more as their sex becomes relatively more abundant (along ordinate axes) and as the benefits of helping increase (between ordinate axes); under haplodiploidy (dashed lines), females help slightly less, and males help slightly more, than under diploidy (solid lines), provided there is an intermediate rate of sib-mating ($0 < s < 1$). The effect of sib-mating, s , depends on the sex in question and on whether helping is voluntary or maternally manipulated. (a) Voluntary helping by females: helping is promoted under intermediate sib-mating. (b) Voluntary helping by males: sib-mating promotes helping. (c) Maternally manipulated helping by females: sib-mating inhibits helping. (d) Maternally manipulated helping by males: sib-mating promotes helping.

LMC, yields an inclusive-fitness benefit $sp_{bro|f}c_m/(N(1-z))$, whereas each brother, by intensifying LMC, yields an inclusive-fitness cost $-s^2p_{bro|f}c_m/(Nz)$ (*cf. Sex allocation*, above). LME has no effect when sib-mating is absent ($s = 0$) or complete ($s = 1$), but otherwise ($0 < s < 1$) it moderately promotes female helping (Fig. S2a, Supporting Information).

Natural selection favours an increase in voluntary helping by males, y , when

$$\underbrace{-p_{self|m} \frac{c_m}{Nz(1-y)}}_{\text{sacrifice effect}} + b_m \left[\underbrace{(1-z)p_{sis|m} \frac{c_f}{N(1-z)} + zp_{bro|m} \frac{c_m}{Nz}}_{\text{sib-rearing effect}} \right] + \underbrace{s^2p_{bro|m} \frac{c_m}{Nz(1-y)}}_{\text{LMC effect}} + b_m \left[\underbrace{(1-z)sp_{bro|m} \frac{c_m}{N(1-z)} + zs^2p_{bro|m} \frac{c_m}{Nz}}_{\text{LME effect}} \right] > 0. \tag{3}$$

The left-hand side gathers the inclusive-fitness effects experienced by a reproductive male who joins a sterile helper caste, which together shape male helping (Fig. 4b). Above,

$p_{self|m} = (2-s)/(4-3s)$, $p_{sis|m} = p_{bro|m} = 1/(4-3s)$ under diploidy, and $p_{self|m} = 1$, $p_{sis|m} = 1/(4-3s)$, $p_{bro|m} = (2-s)/(4-3s)$ under haplodiploidy.

The sacrifice, sib-rearing and LME effects in condition 3 exactly mirror the corresponding effects in condition 2. Hence, as the sex ratio becomes relatively male-biased, male helping is promoted because its direct cost is reduced. However, the symmetry breaks down with respect to LMC: while the LMC effect in condition 2 captures an indirect cost for a female abstaining from mating, the LMC effect in condition 3 captures an indirect benefit for a male abstaining from mating. Specifically, the male's forfeited RV, $c_m/(Nz(1-y))$, yields a corresponding increase in RV for his mate competitors, who are his brothers to the extent s^2 that neither he nor his brothers would disperse before mating, and hence have expected consanguinity $s^2p_{bro|m}$ with the male.

Accordingly, sib-mating – by increasing sibling relatedness, incentivising abstention from LMC, and returning benefits through LME (Fig. S2b, Supporting Information) – promotes a male's willingness to help. Indeed, under sib-mating ($s > 0$),

males are generally more willing to help than females, for an even sex ratio ($z = 1/2$) and equal helping ability ($b_f = b_m$; Fig. 4a and b). And, in contrast with Hamilton's (1964, 1972) haplodiploidy hypothesis, this relative predisposition for male helping may be magnified under haplodiploidy. This is because, under haplodiploidy: (1) inbreeding leads a female to be more consanguineous with herself, increasing her cost of self-sacrifice, but this is not true for males, as a haploid individual cannot be inbred (*cf.* Davies & Gardner 2014); and (2) inbreeding leads males to value brothers more than females do, increasing their willingness to abstain from LMC and their indirect benefits through LME.

Maternally manipulated helping – If mothers control their offspring's investment into helping, then natural selection favours an increase in helping by females when

$$\underbrace{-p_{\text{dau}} \frac{c_f}{N(1-z)(1-x)}}_{\text{sacrifice effect}} + b_f \underbrace{\left[(1-z)p_{\text{dau}} \frac{c_f}{N(1-z)} + zp_{\text{son}} \frac{c_m}{Nz} \right]}_{\text{sib-rearing effect}} - \underbrace{sp_{\text{son}} \frac{c_m}{N(1-z)(1-x)}}_{\text{LMC effect}} + b_f \underbrace{\left[(1-z)sp_{\text{son}} \frac{c_m}{N(1-z)} + zs^2 p_{\text{son}} \frac{c_m}{Nz} \right]}_{\text{LME effect}} > 0, \quad (4)$$

and an increase in helping by males when

$$\underbrace{-p_{\text{son}} \frac{c_m}{Nz(1-y)}}_{\text{sacrifice effect}} + b_m \underbrace{\left[(1-z)p_{\text{dau}} \frac{c_f}{N(1-z)} + zp_{\text{son}} \frac{c_m}{Nz} \right]}_{\text{sib-rearing effect}} + \underbrace{s^2 p_{\text{son}} \frac{c_m}{Nz(1-y)}}_{\text{LMC effect}} + b_m \underbrace{\left[(1-z)sp_{\text{son}} \frac{c_m}{N(1-z)} - zs^2 p_{\text{son}} \frac{c_m}{Nz} \right]}_{\text{LME effect}} > 0. \quad (5)$$

Conditions 4 and 5 may be obtained by substituting into conditions 2 and 3 the consanguinities p_{dau} instead of p_{self} and p_{sis} , and p_{son} instead of p_{self} and p_{bro} , reflecting that, for manipulated helping, natural selection acts on the mother's inclusive fitness rather than that of the helpers. The resulting effect on helping is illustrated in Fig. 4c and d. All else being equal, mothers prefer more helping than potential helpers themselves do when $s < 1$ – therefore, there is potential for parent-offspring conflict over the extent of sib-rearing (Alexander 1974; Trivers 1974; González-Forero 2014). Analogously to voluntary helping, mothers tend to recruit more male helpers in the context of inbreeding ($s > 0$), because recruiting males alleviates LMC, while recruiting females exacerbates LMC; this effect is magnified under haplodiploidy, because inbreeding increases a mother's valuation of her daughters relative to her sons (see *Sex allocation*, above).

Promiscuity and helping – Although we focus on monogamy above, our model allows us to consider promiscuity's effect on sex-specific helping. Under diploidy, promiscuity tends to inhibit voluntary helping by decreasing sibling relatedness. Under haplodiploidy, promiscuity tends to inhibit voluntary helping by females, but has no effect on helping by males, because haploid males are only related to their siblings through their mothers (Fig. S4, Supporting Information). Note that promiscuity does

not affect sex allocation or maternally manipulated helping, because it does not alter a mother's comparative relatedness to her daughters vs. sons (see Supporting Information for details).

Coevolution of sex allocation and sex-biased helping

Because sex allocation depends on the helpfulness of females vs. males (see condition 1), while helping depends on sex allocation (see conditions 2–5), there is potential for coevolution between sex allocation and sex-biased helping. Indeed, whilst both sexes may help when the sex ratio is fixed at a particular value, we find that only one sex helps when we permit these traits to coevolve (Fig. 5).

When sex allocation is fixed at $z = 1/2$, individuals of both sexes may help. For voluntary helping, females and males each help according to their ability (Fig. 5a); for maternally manipulated helping, the mother recruits female and male helpers according to her need (Fig. 5c). In either case, sib-mating tends to promote male helping, an effect which is slightly magnified under haplodiploidy (see *Sex-specific helping*, above).

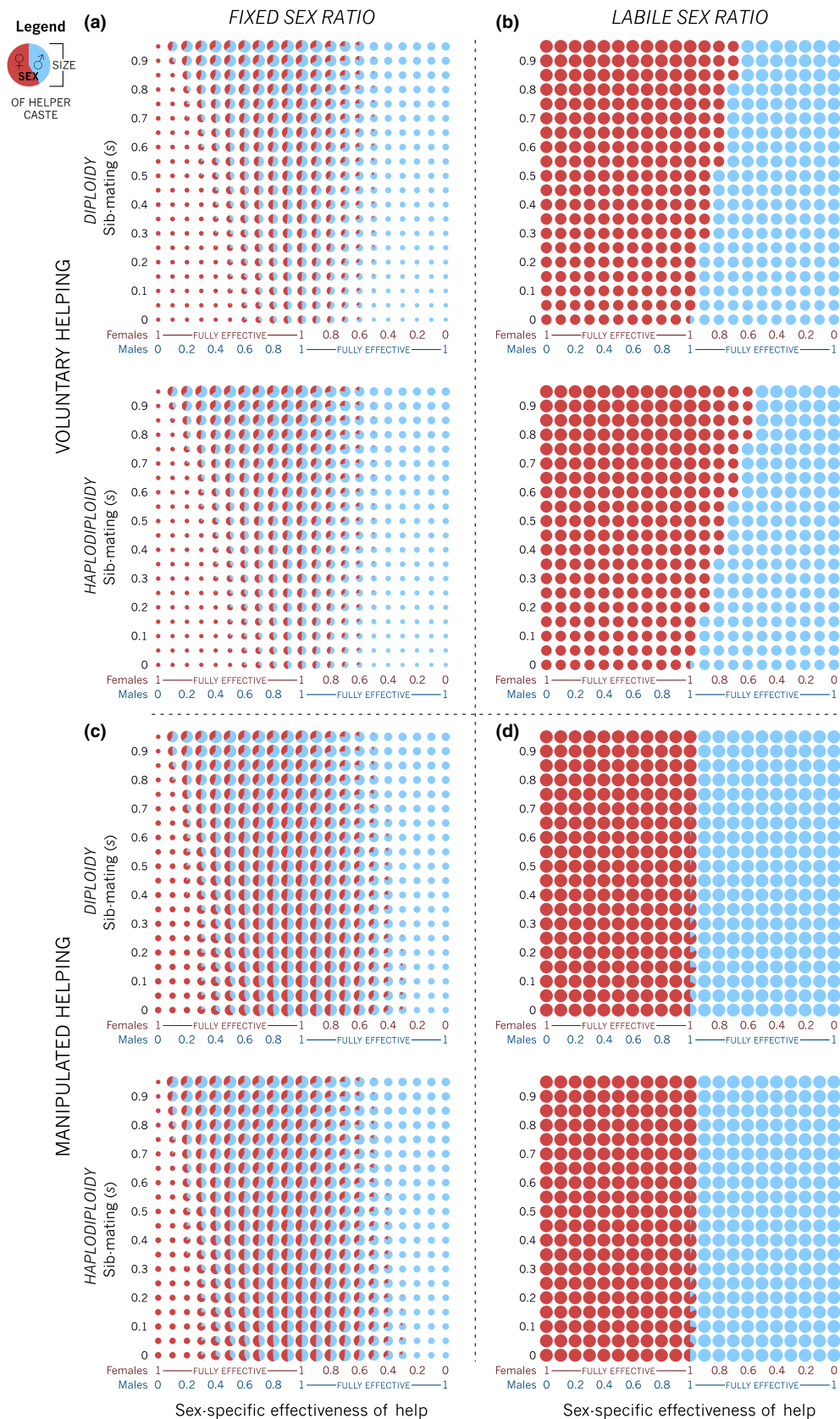
In contrast, when the sex ratio is evolutionarily labile, typically only one sex helps. For voluntary helping, this is because any sex difference in helpfulness ($b_{fx} \neq b_{my}$) attracts a sex-allocation bias favouring the more-helpful sex (due to the LRE effect, condition 1), while any change in sex allocation makes the favoured sex more willing to help, and the disfavoured sex less willing to help (due to the sacrifice effect, conditions 2 and 3). This positive feedback between sex-biased helping and sex-ratio bias ultimately promotes helping by one sex only. Which sex helps may be influenced by several factors but, over some regions of parameter space, both female-only and male-only helping represent possible alternative stable states (see Supporting Information). In particular, in the context of outbreeding ($s = 0$) and no sex bias in ability ($b_f = b_m$), all-female helping and all-male helping are equally likely alternatives. A bias in ability ($b_f \neq b_m$) tends to promote exclusive helping by the more-able sex, while sib-mating ($s > 0$) – by favouring a female-biased sex allocation – tends to promote exclusive helping by females (Fig. 5b).

For maternally manipulated helping, only one sex helps when sex allocation is labile because full control of both sex allocation and helping allows the mother to recruit helpers solely from the more-able sex, adjusting her sex allocation as needed to produce the desired adult sex ratio. Hence, only the more-able sex is expected to help, regardless of ploidy or sib-mating (Fig. 5d). In the absence of sex-specific preadaptation ($b_f = b_m$), the helper sex ratio is selectively neutral from the mother's perspective, and any sex bias may depend on other factors.

Finally, we find that evolutionarily labile sex allocation promotes helping overall, because it allows mothers to invest more in helpers. This result holds regardless of the relative helping ability of females vs. males, except for manipulated helping when females and males are exactly equally preadapted, in which case labile sex allocation has no effect (Fig. 5).

EMPIRICAL SURVEY

Focusing on the origins of sociality, we collected published data from across the social arthropods, including both



primitively social species, where individuals delay dispersal to conduct sib-rearing, and facultatively eusocial species, with non-reproductive helper castes. However, we excluded

eusocial species with complementary totipotency (Crespi & Yanega 1995; Boomsma 2013) as these are highly derived and may display secondarily evolved traits that hinder

Figure 5 Patterns of helping as a function of sex differences in helping ability, sib-mating, diploidy vs. haplodiploidy, voluntary vs. maternally manipulated helping, and fixed vs. labile sex allocation. Each pie chart shows the equilibrium state following the evolution of helping, giving the percentage of helpers who are female (red) vs. male (blue), as well as the size of the helper caste (diameter of pie chart), for a given set of parameters. Each chart is obtained by numerically integrating selection gradients (conditions 1–5) starting from no helping ($x = y = 0$). Sex allocation is either fixed at $z = 1/2$ (panels a and c), or set to its equilibrium value in the absence of helping, then permitted to freely coevolve with helping (panels b and d). Here, we assume a maximum sib-rearing benefit of $b_{\max} = 4$, i.e. $b_f = 4 e_f$ and $b_m = 4 e_m$, where e_f and e_m are the ‘effectiveness of help’ for females and males, respectively (bottom of each plot). Note that differences between diploidy and haplodiploidy *per se* are minor, whereas sex differences in ability have a major influence on the sex of helpers.

straightforward interpretation of helper sex (e.g. sex-specific task specialisation). For each independent origin of social behaviour, we recorded: the sex of helpers; any behavioural sex differences in willingness to help; whether sociality evolved under inbreeding or outbreeding; and ploidy. Finally, we assessed possible sex-specific preadaptation for helping. Following Ross *et al.* (2013), where helping involves brood care, we assumed that the sex or sexes that ancestrally provided parental care are preadapted. Where helpers defend the colony, we assumed preadaptation if one sex is better-equipped for the task, e.g. through superior body size or weaponry. We included multiple species per origin of sociality if there was variation for any trait of interest. Data were analysed using a phylogenetically controlled mixed-model approach using the R packages MCMCglmm (Hadfield & Nakagawa 2010) and MCMCglmmRAM (Hadfield 2015). We estimated a molecular phylogeny for 31 taxa, each covering a separate evolutionary origin, using BEAST (Drummond *et al.* 2012) with published sequences (5929 aligned sites across the following loci: *16S*, *18S*, *28S*, *coi*, *coii*, *cytb*, *ef1a*, *h3*, *wingless*; see Supporting Information for full methodology).

We identified 16 eusocial and 28 primitively social origins of sib-rearing among arthropods (Fig. 1). Remarkably, and in contrast with assumptions of previous theory on the evolution of eusociality, over half of these origins appear in the context of inbreeding and LMC. Our survey also shows that even in species where both sexes help, there are generally subtle sex biases, either numerical or behavioural, and completely unbiased helping is rare. Of the 44 origins we identified, full data were available for 30 (Table S3 and Fig. S11, Supporting Information). Undertaking taxonomically and phylogenetically controlled comparative analyses, we find that sex biases in helping are primarily determined by sex differences in helping ability (Fig. 6a; $p_{\text{MCMC}} < 0.001$ for both analyses), while neither ploidy (phylogenetic $p_{\text{MCMC}} = 0.50$, taxonomic $p_{\text{MCMC}} = 0.996$) nor sib-mating (phylogenetic $p_{\text{MCMC}} = 0.50$, taxonomic $p_{\text{MCMC}} = 0.25$) are significant determinants of helper sex.

A key prediction of our model is that, while both sexes may help if sex allocation is constrained, helping should be restricted to one sex if sex allocation is evolutionarily labile. As there is little direct information concerning which species can bias the sex ratio, we used indirect estimates where necessary, assuming that haplodiploids and any species with ancestral LMC have this ability. We find that, with one exception (the *Austroplatypus* ambrosia beetle), single-sex workers are restricted to taxa able to freely adjust sex allocation, and the association between helper sex bias and sex-ratio lability is significant (phylogenetic $p_{\text{MCMC}} = 0.02$) or marginally non-significant (taxonomic $p_{\text{MCMC}} = 0.07$) across independent origins of helping (Fig. 6b).

DISCUSSION

We have analysed the coevolution of sex allocation and sib-rearing in a demographically explicit mathematical model, contrasting the impact of ploidy vs. preadaptation upon patterns of helping in arthropod societies. We find that ploidy has little effect, while five key aspects of sexual ecology – sex-specific preadaptation, sex-ratio constraints, sib-mating, promiscuity and reproductive autonomy – influence the sex and abundance of helpers. We have assessed the empirical support for and relevance of these predictions by conducting a comparative survey of all known origins of sociality in arthropods.

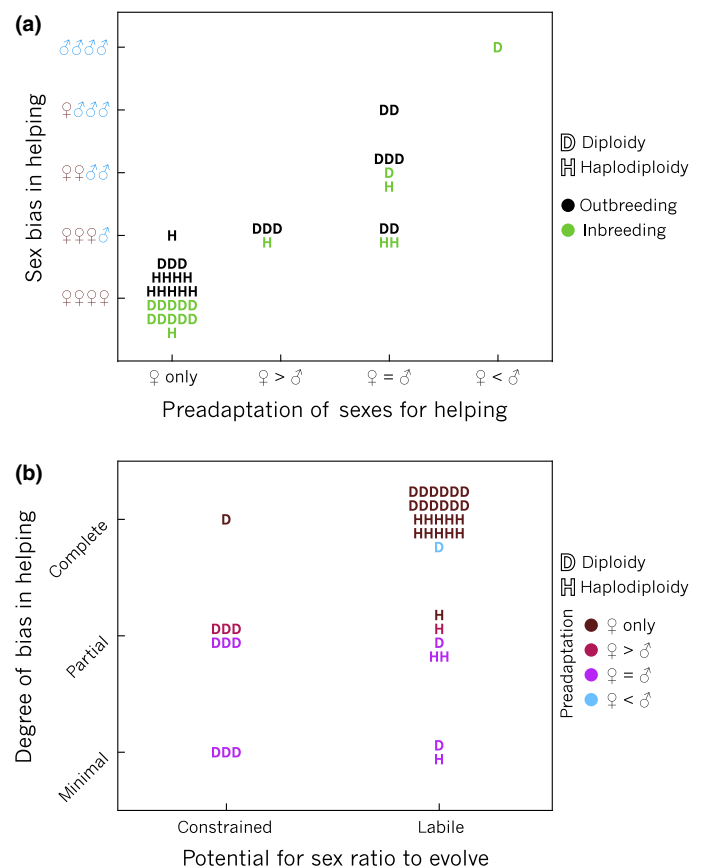


Figure 6 Data from the empirical survey providing a qualitative test of model predictions. (a) Across origins of helping in arthropods for which data are available, sex-specific preadaptation for helping tasks is significantly associated with the sex of helpers (phylogenetic $p_{\text{MCMC}} < 0.001$, taxonomic $p_{\text{MCMC}} < 0.001$). (b) The helper sex ratio tends to exhibit a greater bias towards single-sex helping in clades with an inferred ancestral ability to bias the sex ratio (phylogenetic $p_{\text{MCMC}} = 0.02$, taxonomic $p_{\text{MCMC}} = 0.07$).

Our analysis provides a formal foundation for the ‘preadaptation hypothesis’ that sex biases in helping may reflect ancestral sexual dimorphism for traits co-opted for sib-rearing. In other words, sex-biased sib-rearing – whether by immature reproductives or sterile helpers – is modulated by intrinsic sex differences in helping ability, as established empirically by Ross *et al.* (2013). Innate differences may be expected if, for example, helpers originate as nurses in a taxon with ancestral maternal-only care – as in the aculeate Hymenoptera, where maternal care is widespread (Hamilton 1964; Hölldobler & Wilson 1990; Alexander *et al.* 1991) and sib-rearing derives from brood care redirected towards siblings (Wheeler 1928; Kennedy 1966; Michener 1969; Wilson 1971; Hamilton 1972; Alexander 1974; West-Eberhard 1987; Amdam *et al.* 2006; Toth *et al.* 2007; Boomsma 2007).

Crucially, we have shown that sex differences in helping ability need not be absolute to have a major influence on who helps. Any initial sex difference in helpfulness promotes a sex-ratio bias favouring the more-helpful sex via LRE (Fig. 3), which selects for further-biased helping by comparatively decreasing the more-helpful individuals’ RV (Fig. 4), eventually leading to single-sex helping (Fig. 5). Here, sex allocation impacts upon sib-rearing because helping becomes comparatively more appealing as mating opportunities diminish in value; in contrast, Johnstone & Cant (2008) – who assumed that non-breeders cannot help – found no impact of sex allocation upon helping. In contradistinction to the haplodiploidy hypothesis, our analysis highlights that single-sex helping should emerge by default – and that it is mixed-sex workforces that demand a special explanation, such as relatively constrained sex allocation.

Because sexually dimorphic traits relevant for helping may stem from male–female asymmetries in sexual selection, the mating system, and gametic investment (Queller 1997), sex-specific preadaptation itself reflects a species’ ancestral sexual ecology. We have shown that contemporary sexual ecology also plays a crucial role, as it both drives sex-biased helping directly and generates sex-ratio biases that themselves promote biased helping. In particular, sib-mating, with concomitant inbreeding and LMC, may have a major impact upon sex-specific helping, depending on the species’ ability to adjust the sex ratio. Specifically, under a fixed sex ratio – for example, owing to an inflexible chromosomal mode of sex determination – LMC may drive relatively male-biased helping as an alternative means of diverting resources from male to female reproduction (Fig. 5a and c). In contrast, under an evolutionarily labile sex ratio, LMC may drive female-biased sex allocation, decreasing females’ RV and hence encouraging relatively female-biased helping (Fig. 5b and d). Hence, kin competition among helpers not only influences sex allocation directly (Wild 2006) but also indirectly, by promoting sex-biased helping. Surprising as it is, to our knowledge our analysis is the first to link LMC to the evolution of sex-biased helping, and we suspect this owes to an inordinate focus on the social Hymenoptera leading researchers to believe that inbreeding is of little empirical relevance to the origin of sociality – a misconception that we hope Fig. 1 helps to dispel.

Besides addressing sex biases in helping, our analysis also highlights aspects of sexual ecology that may promote the

emergence of sociality. In addition to suggesting that inflated sororal relatedness explains the all-female workforce of the social Hymenoptera, the haplodiploidy hypothesis suggests that it is also responsible for this group’s multiple independent origins of eusociality (Hamilton 1964, 1972). This view has received criticism on both theoretical and empirical grounds (Trivers & Hare 1976; Craig 1979; Gardner *et al.* 2012), and instead the current consensus is that the presence or absence of strict monogamy is the most important determinant of taxonomic patterns of sociality (Boomsma 2007, 2009, 2013; Hughes *et al.* 2008). This ‘monogamy hypothesis’ suggests that, because full siblings are as related to each other as an individual is to her own offspring, there has been little barrier to the evolution of altruistic sib-rearing in taxa exhibiting strict monogamy, a mating system that is rare especially among iteroparous taxa in which sib-rearing can feasibly arise. This, too, supports the preadaptation view, as it highlights prerequisites for sociality that have not evolved to promote helping: for example, the sperm-storage abilities of the aculeate Hymenoptera enable females to produce multiple broods throughout a potentially long lifetime, despite mating only once. We have confirmed that monogamy dramatically increases selection for sib-rearing, particularly among outbred taxa (Fig. S5, Supporting Information).

The ability to adjust the sex ratio, in addition to its role in magnifying sex biases in helping, also acts to promote helping, by enabling the mother to invest more in helpers. Frank & Crespi (1989) proposed an alternative feedback, with Trivers & Willard’s (1973) effect driving split sex ratios, which – in conjunction with haplodiploidy – then drive female-biased helping. Our model predicts more investment into helping, exhibiting a greater sex bias, than existing models that do not consider coevolution between sex allocation and helping (Pen & Weissing 2000; Wild 2006; Johnstone & Cant 2008). Similar positive feedback was shown by Gardner & Ross (2013), although their model assumed female-only helping from the outset rather than allowing sex-biased helping to evolve from scratch. They noted that an evolutionarily inflexible sex ratio poses a significant barrier to the evolution of eusociality when only females can help, and we have shown that this result extends to both sexes (potentially) helping, whether voluntarily or under maternal manipulation (Fig. 5). This may explain why, among 44 identified origins of sib-rearing in arthropods, 37 (84%) occurred in clades with an inferred ancestral ability to adjust the sex ratio.

We also propose that sib-mating may promote sociality in arthropods (Fig. 5; Figs. S5 and S6, Supporting Information). The effect of inbreeding on the evolution of sib-rearing has been considered before: because it reduces relatedness asymmetries between a haplodiploid female and her siblings of either sex (Hamilton 1972; Crozier & Pamilo 1996); because it may influence the speed or favourability of the evolution of altruism under particular genetic architectures (Michod 1993); or because cyclical inbreeding could result in individuals being more related to (inbred) siblings than to their potential (outbred) offspring (Hamilton 1972; Bartz 1979; Chapman 2003; *cf.* Myles & Nutting 1988). Here, we have outlined a novel mechanism by which inbreeding may promote altruistic sib-rearing, through the particular ecological context of LMC. In

this context, LME may promote helping both by increasing an individual's willingness to help and by further promoting a sex-ratio bias favouring the more-helpful sex (Figs. S1 and S2, Supporting Information). Furthermore, male helping in particular is promoted via the inclusive-fitness benefits of abstaining from LMC: a male who gives up breeding to help does not completely forfeit his genetic interest in a potential mate's offspring if she simply mates with his brother instead. It is suggestive that, among 44 identified origins of sociality, 24 (55%) have occurred in clades ancestrally associated with sib-mating (Fig. 1).

A further aspect of sexual ecology is whether individuals make their own breeding decisions (Alexander 1974; Michener & Brothers 1974). Maternally manipulated helping is suggested to be more readily favoured than voluntary helping (Alexander 1974; Charlesworth 1978; Charnov 1978) and, indeed, we find that maternal manipulation promotes helping, particularly under outbreeding (Fig. 5). Nonetheless, maternally manipulated helping – while theoretically plausible – may not readily explain eusociality's absence outwith ancestrally monogamous taxa (*cf.* González-Forero & Gavrillets 2013).

Although our comparative survey supports the prediction that sex-specific preadaptation explains sex biases in helping (Fig. 6), single-sex helping is not always empirically observed in taxa exhibiting a labile sex ratio. We suggest three possible reasons for this. First, helping may yield direct-fitness benefits, incentivising individuals of both sexes to engage in nest defence, cooperative feeding, or (cryptic) parental care. Second, the cost of reproduction under local mating may be sufficiently low that there is a point at which further investment in helping by a particular sex is disfavoured, arresting the feedback between sex allocation and sex-biased helping. Third, if helping is manipulated and there is no significant sex bias in ability, mothers may not be selected to recruit helpers from one sex preferentially.

In our model we have taken sex-specific helping ability as given and not subject to evolution. However, helpers, once established, will be favoured to improve their helping ability. Accordingly, empirically measured sex differences in helping ability may be partly a consequence, not a cause, of sex differences in willingness to help. Moreover, a constrained sex ratio not only promotes mixed-sex helping but, by inducing strong selection for improvement in the less-able sex, may also act to abolish sex differences in helping ability, further obscuring the direction of causality. However, it is likely that extant sex differences in ability reflect the direction, if not the magnitude, of ancestral sex differences that would have driven the initial establishment of sex-biased helping. In this vein, recent theoretical work has shown that voluntary helping can arise as an elaboration of manipulated helping when helping efficiency evolves over time (González-Forero 2014). In such a case, our model would predict that contemporary sex biases in helping reflect ancestral biases, while contemporary investment in helping reflects current helping efficiency.

More generally, our analysis shows that haplodiploidy *per se* has little relevance to the evolution of sex-specific helping; and when it does impact the sex of helpers – *i.e.*, under sib-mating and/or promiscuity – it may have the opposite effect

to that predicted by Hamilton, inhibiting helping by females and promoting helping by males. Rather, the main impact of haplodiploidy upon the evolution of eusociality appears to be (1) by its providing a ready means of sex-ratio adjustment (de la Filia *et al.* 2015), which magnifies both sex biases and investment in helping; and (2) by its preadapting taxa for inbreeding ecologies – which may promote sib-rearing – by purging recessive alleles associated with inbreeding depression and by allowing a sex-ratio response to LMC.

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AUTHORSHIP

NGD, LR and AG designed the study and wrote the manuscript; NGD led the mathematical analysis; and LR led the phylogenetic analysis.

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