

## Research



**Cite this article:** Kennedy P, Radford AN. 2020 Sibling quality and the haplodiploidy hypothesis. *Biol. Lett.* **16**: 20190764. <http://dx.doi.org/10.1098/rsbl.2019.0764>

Received: 18 October 2019

Accepted: 12 February 2020

### Subject Areas:

behaviour, ecology, evolution

### Keywords:

eusociality, haplodiploidy, altruism

### Author for correspondence:

P. Kennedy

e-mail: [patrick.kennedy@bristol.ac.uk](mailto:patrick.kennedy@bristol.ac.uk)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4867224>.

## Evolutionary biology

# Sibling quality and the haplodiploidy hypothesis

P. Kennedy and A. N. Radford

School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

PK, 0000-0002-2524-6192; ANR, 0000-0001-5470-3463

The ‘haplodiploidy hypothesis’ argues that haplodiploid inheritance in bees, wasps, and ants generates relatedness asymmetries that promote the evolution of altruism by females, who are less related to their offspring than to their sisters (‘supersister’ relatedness). However, a consensus holds that relatedness asymmetry can only drive the evolution of eusociality if workers can direct their help preferentially to sisters over brothers, either through sex-ratio biases or a pre-existing ability to discriminate sexes among the brood. We show via a kin selection model that a simple feature of insect biology can promote the origin of workers in haplodiploids without requiring either condition. In insects in which females must found and provision new nests, body quality may have a stronger influence on female fitness than on male fitness. If altruism boosts the quality of all larval siblings, sisters may, therefore, benefit more than brothers from receiving the same amount of help. Accordingly, the benefits of altruism would fall disproportionately on supersisters in haplodiploids. Haplodiploid females should be more prone to altruism than diploid females or males of either ploidy when altruism elevates female fitness especially, and even when altruists are blind to sibling sex.

## 1. Introduction

In 1964, Hamilton proposed that haplodiploidy has been a major driving force behind the multiple origins of eusociality in the Hymenoptera (bees, wasps and ants) [1,2]. Males are haploid, inheriting genes only from the mother, while females are diploid, inheriting genes from both parents [3]. In monogamous haplodiploids, sisters share their entire haploid father’s genome, while maternal alleles have a 50:50 chance of being shared by sisters. Accordingly, a female is related to her sisters by  $r = 0.75$  (i.e. 0.5 from the father and  $0.5 \times 0.5$  from the mother). This ‘supersister’ relatedness is 50% greater than a female’s relatedness to her own offspring ( $r = 0.5$ ), suggesting that a female should prefer to raise sisters than attempt personal reproduction [1,2,4].

The haplodiploidy hypothesis has been repeatedly questioned [5–13], and other reasons for a possible link between haplodiploidy and female altruism have been suggested in its place (e.g. [14–16]). Theoretical objections have largely centred on the problem that the haplodiploidy hypothesis requires helper females to bias altruism towards sisters (sister-biased helping). If altruism is received equally by sisters and brothers, haplodiploids should be no more prone to eusociality than diploids (in which both sexes are diploid and produced sexually). This is because, under haplodiploidy, a female’s relatedness to brothers is only  $r = 0.25$ : indiscriminate sibling altruism will produce an average recipient relatedness of  $r = 0.5$ . Under both haplodiploidy and diploidy, then, there would be no asymmetry in relatedness to offspring and siblings. Trivers and Hare [8] argued that sister-biased helping could arise if helpers tend to inhabit nests with a female-biased brood sex ratio, but noted that an increasingly female bias in the population diminishes the value of rearing sisters

and amplifies the value of rearing brothers. Accordingly, female sex-ratio biases in nests with helpers must be more extreme than elsewhere in the population (split sex ratios) for altruism to be promoted more by haplodiploidy than by diplodiploidy [8,17]. Because split sex ratios arise only under rare and often complex conditions [5], this requirement led to a consensus that the haplodiploidy hypothesis is an unlikely driver of eusociality. Recently, Rautiala *et al.* [18] have argued that split sex ratios are unnecessary, and haplodiploidy can drive eusociality at all sex ratios—on the crucial assumption that the first-evolving workers discriminate among brood by directing their help preferentially towards females ('the ability for helpers to treat sisters and brothers differently' [18]). Although sex discrimination occurs in simple eusocial species (e.g. [19]) and is familiar in more advanced eusocial taxa [20,21], it remains unknown whether this ability evolved subsequent to the evolution of workers or characterized workers at the dawn of sociality.

Here, we highlight a scenario in which the classic haplodiploidy effect [1] can drive eusociality without split sex ratios and without females needing to treat developing sisters and brothers differently. Models of eusocial evolution have focused on the *quantity* of siblings raised by helpers [8,18,22], but recent empirical studies of facultatively and primitively social insects have found that effects on sibling quantity alone can be too small to drive voluntary altruism [23,24]. We suggest a need to incorporate additional effects that helpers may have on the *quality* of siblings.

Across vertebrates and insects, the reproductive successes of males and females can depend differently on body condition [25,26], which can be influenced by the receipt of resources from helpers before reproductive maturity [27]. There has been no systematic and direct comparison of the extent to which male versus female fitness depends on body condition in nest-founding insects, and so the strength and sex asymmetry of condition-dependence remains largely unknown. However, greater condition-dependent variability in female fitness may plausibly arise when female nest-founding (including larval provisioning and any necessary female-only overwinter survival) is energetically challenging [27–30], and especially in contexts involving relatively limited scope for male–male competition or mate choice [29]. In nest-founding insects without biparental care, a female must face the extreme challenge of founding a new nest and raising larvae to adulthood [31] in addition to mating; a male must only mate. Empirical results suggest that higher condition females (larger, with more fat reserves acquired during development) have a stronger chance than those in the poorer condition of being successful nest-builders [32,33], and reveal heavy reliance on energy reserves by foundress females [31,34].

Using a kin selection model, we explore whether female-biased condition-dependence alters thresholds for eusociality under different ploidies. We focus on a situation requiring minimal assumptions about worker phenotypes: we assume that (1) the ability to discriminate male and female brood [18] is absent, (2) there are no pre-existing biases in the ability of males and females to provide help [22] and (3) mothers retain control over their broods' sex ratios. Helpers may increase the condition of all brood, which is likely to benefit females disproportionately. In this context, we find that a helper should not only aim to amplify the quantity of siblings but also to elevate the quality of sisters, maximizing the quantity of nieces and nephews.

## 2. Model

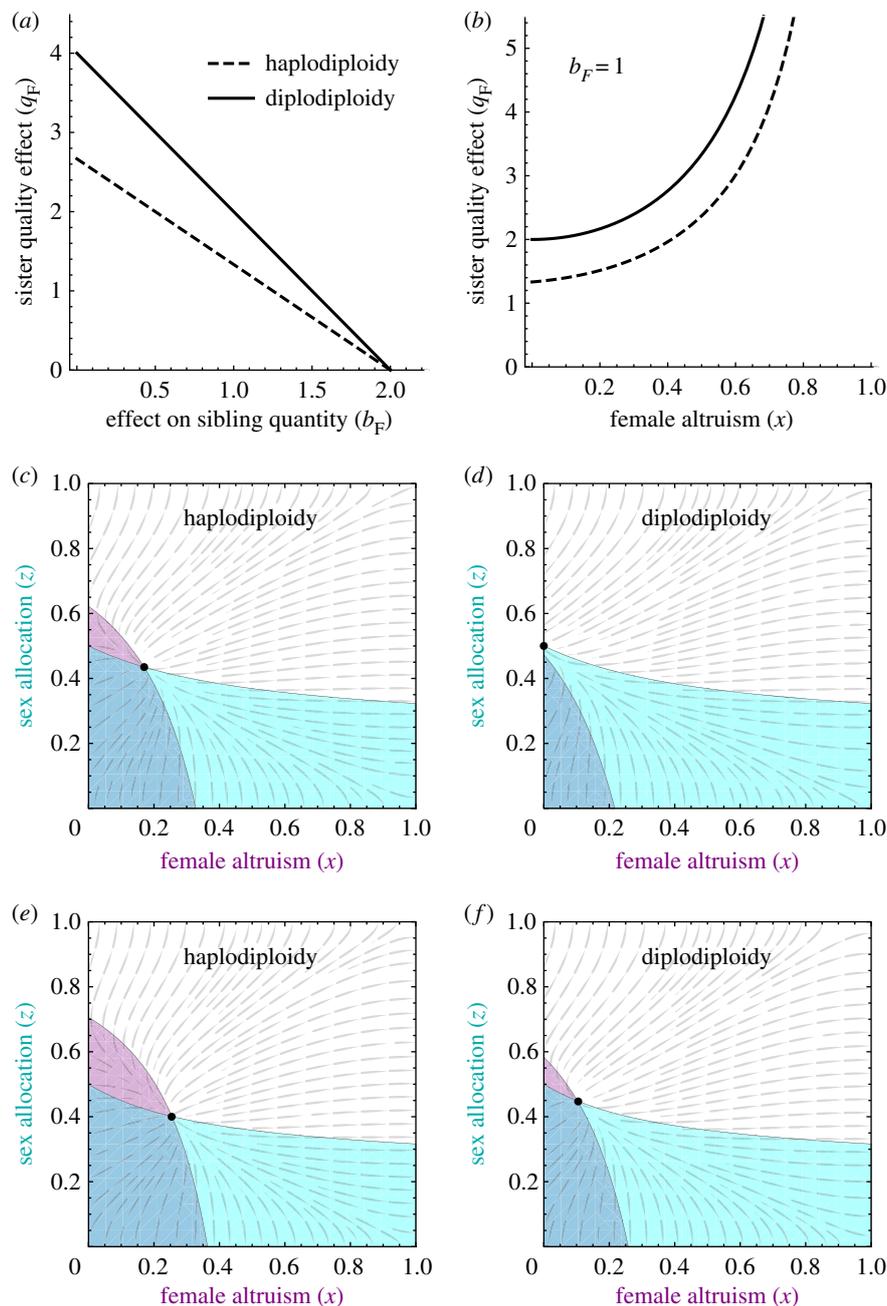
We assume a monogamous, outbreeding population. We build on the framework of Davies *et al.* [22], who analyse the evolution of eusociality under different ploidies, to incorporate sex-asymmetrical condition-dependence. Females develop to be sterile helpers with probability  $x$  (with a population average  $\bar{x}$ ), males develop to be sterile helpers with probability  $y$  (with a population average  $\bar{y}$ ) and the brood sex ratio (the proportion male) is  $z$  (with a population average  $\bar{z}$ ). Help  $h$  is the sum of help from male and female helpers. We allow altruists to influence two different (not mutually exclusive) components of the fitness of brood in the nest. First, helpers may raise the probability  $B = B(h)$  that brood survive to reproductive maturity (i.e. helpers may raise the quantity of adult reproductive siblings). We follow Davies *et al.* [22] in denoting the fitness effect of female help on relative brood survival to reproductive maturity as  $b_F = e_F(dB/dh|_{h=\bar{h}})/B(\bar{h})$ , where  $e_F$  denotes helping efficiency of females and  $B(\bar{h})$  is the population-average survival to reproductive maturity. Likewise,  $b_M = e_M(dB/dh|_{h=\bar{h}})/B(\bar{h})$  denotes the fitness effect of male help on relative brood survival to reproductive maturity, where  $e_M$  denotes helping efficiency of males. Second, helpers may raise the probability  $Q = Q(h)$  that, given a female brood member has reached reproductive maturity, she will successfully found a new nest (helpers, therefore, may influence the quality of adult reproductive sisters). We let the fitness effect of female help on female relative nest-founding success be  $q_F = e_F(dQ/dh|_{h=\bar{h}})/Q(\bar{h})$ , where  $Q(\bar{h})$  is the population-average nest-founding success. Likewise,  $q_M = e_M(dQ/dh|_{h=\bar{h}})/Q(\bar{h})$  denotes the fitness effect of male help on female relative nest-founding success. Nest-founding success is a female-specific trait, affected by the amount of help a nest-founding female receives before her own reproductive maturity.

In the electronic supplementary material, we show that selection favours a small increase in female helping when:

$$(b_F + q_F)(1 - \bar{x})(1 - \bar{z})v_F p_{\text{sis}|F} + b_F(1 - \bar{y})\bar{z}v_M p_{\text{bro}|F} > v_F p_{\text{self}|F} \quad (2.1)$$

where consanguinities ( $p$ ) denote the probabilities with which a random allele in the social partner is identical by descent to a random allele at the same locus in the actor [35]. Assuming monogamy, haplodiploid consanguinities from a focal female are  $p_{\text{self}|F} = 1/2$  to self,  $p_{\text{sis}|F} = 3/8$  to a sister and  $p_{\text{bro}|F} = 1/4$  to a brother [5]. Diplodiploid consanguinities are  $p_{\text{self}|F} = 1/2$  to self and  $p_{\text{sis}|F} = p_{\text{bro}|F} = 1/4$  to siblings. Reproductive females and reproductive males have individual reproductive values  $v_F$  and  $v_M$ , respectively (a measure of the probability with which males and females contribute to the distant future gene pool; see electronic supplementary material). The indirect fitness benefits of developing as a sterile altruist are on the left-hand side of inequality 2.1. The direct fitness cost (the loss of the focal individual's own opportunity to reproduce, valued at  $v_F p_{\text{self}|F}$ ) is on the right-hand side. The actor's sacrifice results in  $b_F(1 - \bar{x})(1 - \bar{z})$  additional reproductive sisters and  $b_F(1 - \bar{y})\bar{z}$  additional reproductive brothers, and an addition of nieces and nephews equal in value to  $q_F(1 - \bar{x})(1 - \bar{z})$  reproductive sisters.

Holding  $b_F$  fixed, the threshold benefit levels in terms of improvements to sister quality required to drive a small



**Figure 1.** When help raises the future quality of larval sisters especially, haplodiploid females are more prone to altruism than diploids. (a) Threshold number (required for the invasion of altruism) of additional nieces and nephews from improved quality of sisters by a focal female becoming a sterile altruist in a non-social population ( $\bar{x} = \bar{y} = 0$ ) with an equal sex ratio ( $\bar{z} = 1/2$ ), for different effects on the quantity of siblings ( $b_F$ ). (b) The threshold effect on sister quality for further female altruism ( $x$ ) as altruism rises in the population. The plotted line is found by setting the value of the candidate convergence stable sex allocation  $\bar{z}$  to that which corresponds to altruism level  $\bar{x}$ . Results are shown for  $b_F = 1$  as an illustrative value. (c,d) Increased sex allocation to males is favoured in the blue area; increased female altruism is favoured in the purple areas. Dots denote endpoint equilibria. As female altruists evolve, mothers bias the sex ratio towards the more helpful sex (females). Here, haplodiploids evolve helpers while diploids do not. We plot results for linear relationships between helping ( $h$ ) and quantity ( $B$ ) and quality ( $Q$ ), where  $B = \alpha_B + \beta_B h$  (for  $\alpha_B = 0.5$  and  $\beta_B = 0.2$ ) and  $Q = \alpha_Q + \beta_Q h$  (for  $\alpha_Q = 0.05$  and  $\beta_Q = 0.15$ ). (e,f) Raising the effect on sister quality ( $\beta_Q = 0.2$ ) allows helpers to evolve in diploids, but boosts altruism further in haplodiploids.

rise in helping by females are for haplodiploids and diploids, respectively:

$$q_{\text{HapF}} = \frac{2}{3} \left( \frac{2}{(1-\bar{x})(1-\bar{z})} - 2b_F \right) \quad (2.2)$$

and

$$q_{\text{DipF}} = \frac{2}{(1-\bar{x})(1-\bar{z})} - 2b_F. \quad (2.3)$$

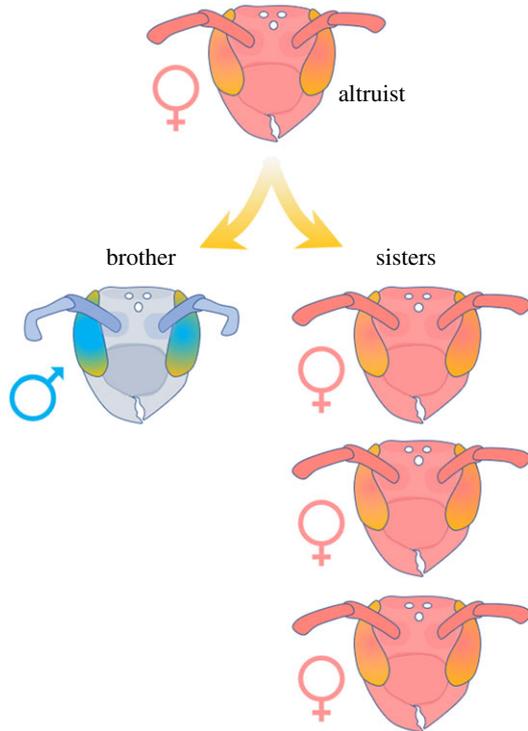
In a non-social population ( $\bar{x} = \bar{y} = 0$ ) with an even sex ratio ( $\bar{z} = 1/2$ ),  $q_{\text{HapF}}$  and  $q_{\text{DipF}}$  can be interpreted as the

number of additional nephews and nieces (resulting from the sibling quality-boosting effect of becoming a sterile altruist) required to promote the initial invasion of altruists.

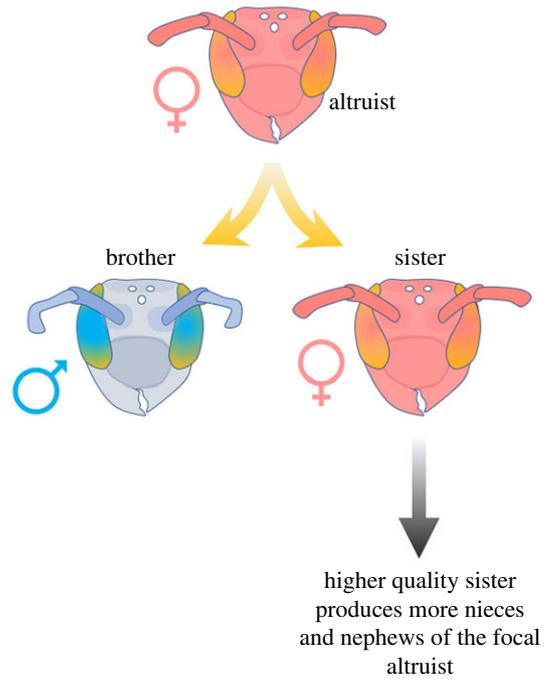
Next, we evaluate the costs and benefits of altruism ( $y$ ) by males. Solving for the fitness effects (see electronic supplementary material), selection favours a small increase in male altruism when, for both diploid and haplodiploid males:

$$(b_M + q_M)(1-\bar{x})(1-\bar{z})v_{\text{FPsis|M}} + b_M(1-\bar{y})\bar{z}v_{\text{Mbro|M}} > v_{\text{Mself|M}}. \quad (2.4)$$

(a) haplodiploidy hypothesis with effects on sibling quantity relies on help being preferentially directed to sisters



(b) haplodiploidy hypothesis with effects on sibling quality does not require sister-biased helping



**Figure 2.** Two routes to eusociality. (a) The classic view of altruism is that it increases sibling quantity. (b) Altruism may also increase sibling quality, especially benefitting nest-building females.

Assuming monogamy, diplo-diploid consanguinities from a focal male are  $p_{\text{self|M}} = 1/2$  and  $p_{\text{sis|M}} = p_{\text{bro|M}} = 1/4$ , while haplodiploid consanguinities are  $p_{\text{self|M}} = 1$ ,  $p_{\text{sis|M}} = 1/4$  and  $p_{\text{bro|M}} = 1/2$ . Holding  $b_M$  fixed, the threshold benefit level in terms of sister quality required to drive a small rise in helping by males of either ploidy is:

$$q_{\text{HapM}} = q_{\text{DipM}} = \frac{2}{\bar{z}(1 - \bar{y})} - 2b_M. \quad (2.5)$$

Thus, for instance, consider a non-social population ( $\bar{x} = \bar{y} = 0$ ) with unbiased sex ratios ( $\bar{z} = 1/2$ ), in the case where helpers will have no effect on the quantity of siblings produced ( $b_F = b_M = 0$ ). The thresholds for the invasion of altruism (due to the effects of sex-indiscriminate helping increasing female quality) are:

$$\begin{cases} q_{\text{HapF}} = 2.6 & \text{for haplodiploid females} \\ q_{\text{DipF}} = 4 & \text{for diplo-diploid females} \\ q_{\text{HapM}} = q_{\text{DipM}} = 4 & \text{for males of either ploidy.} \end{cases}$$

These thresholds can be understood in terms of life-for-life relatedness [5]: when  $\bar{z} = 1/2$ , life-for-life relatedness to a sister's offspring (nephews and nieces) is 0.375 for a haplodiploid female but 0.25 for a diplo-diploid female. Life-for-life relatedness to oneself is 1. To break even when sacrificing her reproduction, a haplodiploid female's altruism must then result in  $1/0.375 = 2.6$  additional nieces and nephews through the improved quality of her reproductive sisters, but a diplo-diploid female's help must result in  $1/0.25 = 4$  additional nieces and nephews. A smaller boost to the quality of sisters ( $q_F$ ) is required to justify altruism for haplodiploid females than for other actor types, unless altruists are able to provide a sufficient boost to sibling quantity ( $b_F$  and  $b_M$ ) to make boosts to sibling quality unnecessary ( $q_F = 0$ , which occurs at  $b_F = 2$  for the

initial invasion of altruists; figure 1a). The benefit thresholds for haplodiploid females (dashed lines in figure 1b;  $q_{\text{HapF}}$ ) are lower than those required for diplo-diploid females (solid lines in figure 1b;  $q_{\text{DipF}}$ ) throughout the invasion of altruists ( $\bar{x}$  ranging from 0 to 1).

As helpers evolve, mothers are expected to bias offspring sex ratios in favour of the more helpful sex [15,22]. We therefore plot the coevolution of sex ratios and female altruism in figure 1c-f. When help boosts sister quality especially, haplodiploids can evolve female altruism when diplo-diploids cannot (figure 1c,d). When the boost to sister quality is enough to drive altruism in diplo-diploids, haplodiploids evolve a higher level of female altruism than diplo-diploids (figure 1e,f).

### 3. Discussion

We find that haplodiploid females enjoy lower thresholds for altruism, in comparison to either diplo-diploid females or males of either ploidy, on the condition that staying to provision the brood increases the quality of sisters more than that of brothers (figure 2). This effect arises even in the absence of split sex ratios [8] or helpers preferentially biasing help towards one sex in the brood [18]. A major bottleneck in the success or failure of a primitive social insect colony may be the hopeful queen's nest-founding quality, affected by the level of help she received in her own development. This is similar to the effects of sunk-cost hysteresis in economics [36]: initiating a new nest (a firm entering the market) demands a huge expenditure of effort, but maintaining an established nest (a firm trading in the market) is relatively easier. At the dawn of sociality, a large effect of workers' help may in principle not be visible until the following

generation, as higher levels of worker help may result in more successful future nest-founding by sibling queens.

A role for sex-asymmetrical condition-dependence has previously been proposed for the haplodiploidy hypothesis. In this verbal 'synergism model', Frank and Crespi [27] suggest that Trivers–Willard effects [26] drive split sex ratios. First, helpers increase sibling condition. Then, mothers with helpers evolve to adjust sex ratios towards daughters, who benefit most from the high condition. Resulting split sex ratios increase selection for helping (by increasing recipient relatedness). The synergism model assumes that helpers have already evolved (and so can explain their maintenance and spread but not origin), and the necessity of split sex ratios has been challenged [18]. Our model shows that condition-dependence can also play a more fundamental role, not only amplifying the spread of altruism by haplodiploid females [27] but driving its origins in populations without sex-ratio biases.

Empirical work is needed to assess the general plausibility of the premise that nest-founding females experience higher condition-dependent variability in reproductive success than males. In scenarios where males face intense male–male competition [37] or where post-insemination sperm survival is highly dependent on male quality [38], this asymmetry may be lessened or even reversed. Conversely, conditions in which body condition appears to affect female fitness profoundly have been repeatedly documented [27,31,32,39–41]. The hypothetical effects of female-biased condition-dependence in nest-building insects raise several empirical questions. First, is condition-dependence more acute at temperate latitudes, where females can be filtered for quality by hibernation [31]? Second, does variable maternal condition at reproduction lead to Trivers–Willard effects [25,26], altering indirect fitness pay-offs for female helpers? Third, do mothers face quantity–quality

trade-offs in the brood, favouring smaller broods before helpers evolve in order to ensure sufficient *per capita* resources fall on daughters to sustain competitiveness? Fourth, does the limited help received by first-emerging daughters lead to a relatively 'subfertile' class [42] for whom altruism is the best available option? Fifth, when benefits of altruism arise through boosting sibling quality, to what extent does any redundant resource consumption by males (having less need than females) act as a constraint on the evolution of altruism in general, regardless of ploidy? Lastly, does load lightening by first helper brood compensate for poor condition in foundress females, reducing the importance of female condition as sociality evolves?

In summary, we highlight a simple effect capable of promoting higher levels of altruism in haplodiploids than in diploids without requiring split sex ratios [8], sex differences in helping efficiency [22], or strategic targeting of help to one sex in the brood [18]. Our aim is not to challenge the plausibility of sister-biased helping at the origin of eusociality, but rather to highlight that—contrary to a prevailing consensus—such a bias is not vital for the haplodiploidy hypothesis.

**Data accessibility.** This article has no additional data.

**Authors' contributions.** P.K. and A.N.R. conceived and drafted the paper. Both authors approved the final version of the manuscript and agree to be held accountable for the work therein.

**Competing interests.** We declare we have no competing interests.

**Funding.** This work was supported by ERC Consolidator Grant 682253 (to A.N.R.).

**Acknowledgements.** We are grateful to N. Davies, P. Rautiala, A. Higginson, T. Linksvayer, R. Bonduriansky and an anonymous reviewer for comments and to N. Davies for suggesting an intuitive measure of nieces and nephews.

## References

- Hamilton WD. 1964 The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7**, 17–52. (doi:10.1016/0022-5193(64)90039-6)
- Hamilton WD. 1972 Altruism and related phenomena, mainly in social insects. *Annu. Rev. Ecol. Syst.* **3**, 193–232. (doi:10.1146/annurev.es.03.110172.001205)
- Heimpel GE, de Boer JG. 2008 Sex determination in the Hymenoptera. *Annu. Rev. Entomol.* **53**, 209–230. (doi:10.1146/annurev.ento.53.103106.093441)
- Bourke AFG. 2011 The validity and value of inclusive fitness theory. *Proc. R. Soc. B* **278**, 3313–3320. (doi:10.1098/rspb.2011.1465)
- Gardner A, Alpedrinha J, West SA. 2012 Haplodiploidy and the evolution of eusociality: split sex ratios. *Am. Nat.* **179**, 240–256. (doi:10.1086/663683)
- Rautiala P, Helanterä H, Puurtinen M. 2014 Unmatedness promotes the evolution of helping more in diploids than in haplodiploids. *Am. Nat.* **184**, 318–325. (doi:10.1086/677309)
- Ross L, Gardner A, Hardy N, West SA. 2013 Ecology, not the genetics of sex determination, determines who helps in eusocial populations. *Curr. Biol.* **23**, 2383–2387. (doi:10.1016/j.cub.2013.10.013)
- Trivers RL, Hare H. 1976 Haplodiploidy and the evolution of the social insects. *Science* **191**, 249–263. (doi:10.1126/science.1108197)
- Gadagkar R. 1991 Demographic predisposition to the evolution of eusociality: a hierarchy of models. *Proc. Natl. Acad. Sci. USA* **88**, 10 993–10 997. (doi:10.1073/pnas.88.24.10993)
- Nowak MA, Tarnita CE, Wilson EO. 2010 The evolution of eusociality. *Nature* **466**, 1057–1062. (doi:10.1038/nature09205)
- Evans HE. 1977 Extrinsic versus intrinsic factors in the evolution of insect sociality. *Bioscience* **27**, 613–617. (doi:10.2307/1297657)
- Lin N, Michener CD. 1972 Evolution of sociality in insects. *Q. Rev. Biol.* **47**, 131–159. (doi:10.1086/407216)
- Alpedrinha J, West SA, Gardner A. 2013 Haplodiploidy and the evolution of eusociality: worker reproduction. *Am. Nat.* **182**, 421–438. (doi:10.1086/671994)
- Fromhage L, Kokko H. 2011 Monogamy and haplodiploidy act in synergy to promote the evolution of eusociality. *Nat. Commun.* **2**, 397. (doi:10.1038/ncomms1410)
- Gardner A, Ross L. 2013 Haplodiploidy, sex-ratio adjustment, and eusociality. *Am. Nat.* **181**, E60–E67. (doi:10.1086/669147)
- Reeve HK. 1993 Haplodiploidy, eusociality and absence of male parental and alloparental care in Hymenoptera: a unifying genetic hypothesis distinct from kin selection theory. *Phil. Trans. R. Soc. Lond. B* **342**, 335–352. (doi:10.1098/rstb.1993.0163)
- Grafen A. 1986 Split sex ratios and the evolutionary origins of eusociality. *J. Theor. Biol.* **122**, 95–121. (doi:10.1016/S0022-5193(86)80227-2)
- Rautiala P, Helanterä H, Puurtinen M. 2019 Extended haplodiploidy hypothesis. *Evol. Lett.* **3**, 263–270. (doi:10.1002/evl3.119)
- Packer L, Owen RE. 1994 Relatedness and sex ratio in a primitively eusocial halictine bee. *Behav. Ecol. Sociobiol.* **34**, 1–10. (doi:10.1007/BF00175452)
- Bourke AFG. 2015 Sex investment ratios in eusocial Hymenoptera support inclusive fitness theory. *J. Evol. Biol.* **28**, 2106–2111. (doi:10.1111/jeb.12710)
- Meunier J, West SA, Chapuisat M. 2008 Split sex ratios in the social Hymenoptera: a meta-analysis. *Behav. Ecol.* **19**, 382–390. (doi:10.1093/beheco/arm143)

22. Davies NG, Ross L, Gardner A. 2016 The ecology of sex explains patterns of helping in arthropod societies. *Ecol. Lett.* **19**, 862–872. (doi:10.1111/ele.12621)
23. Rehan SM, Richards MH, Adams M, Schwarz MP. 2014 The costs and benefits of sociality in a facultatively social bee. *Anim. Behav.* **97**, 77–85. (doi:10.1016/j.anbehav.2014.08.021)
24. Kapheim KM, Nonacs P, Smith AR, Wayne RK, Wcislo WT. 2015 Kinship, parental manipulation and evolutionary origins of eusociality. *Proc. R. Soc. B* **282**, 20142886. (doi:10.1098/rspb.2014.2886)
25. Trivers RL, Willard DE. 1973 Natural selection of parental ability to vary the sex ratio offspring. *Science* **179**, 90–92. (doi:10.1126/science.179.4068.90)
26. Schindler S, Gaillard JM, Grüning A, Neuhaus P, Traill LW, Tuljapurkar S, Coulson T. 2015 Sex-specific demography and generalization of the Trivers–Willard theory. *Nature* **526**, 249–252. (doi:10.1038/nature14968)
27. Frank SA, Crespi BJ. 1989 Synergism between sib-rearing and sex ratio in Hymenoptera. *Behav. Ecol. Sociobiol.* **24**, 155–162. (doi:10.1007/BF00292098)
28. Strohm E, Linsenmair KE. 1997 Low resource availability causes extremely male-biased investment ratios in the European beewolf, *Philanthus triangulum* F. (Hymenoptera, Sphecidae). *Proc. R. Soc. Lond. B* **264**, 423–429. (doi:10.1098/rspb.1997.0060)
29. Seidelmann K, Ulbrich K, Mielenz N. 2010 Conditional sex allocation in the red mason bee, *Osmia rufa*. *Behav. Ecol. Sociobiol.* **64**, 337–347. (doi:10.1007/s00265-009-0850-2)
30. Leathwick DM. 1997 Growth and development of queen colonies of *Vespa germanica* and *V. vulgaris*. *New Zeal. J. Zool.* **24**, 17–23. (doi:10.1080/03014223.1997.9518102)
31. Weissel N, Mitesser O, Poethke HJ, Strohm E. 2012 Availability and depletion of fat reserves in halictid foundress queens with a focus on solitary nest founding. *Insectes Soc.* **59**, 67–74. (doi:10.1007/s00040-011-0189-3)
32. Harris RJ, Beggs JR. 1995 Variation in the quality of *Vespa vulgaris* (L.) queens (Hymenoptera: Vespidae) and its significance in wasp population dynamics. *New Zeal. J. Zool.* **22**, 131–142. (doi:10.1080/03014223.1995.9518030)
33. Gadagkar R, Bhagavan S, Chandrashekara K, Vinutha C. 1991 The role of larval nutrition in pre-imaginal biasing of caste in the primitively eusocial wasp *Ropalidia marginata* (Hymenoptera: Vespidae). *Ecol. Entomol.* **16**, 435–440. (doi:10.1111/j.1365-2311.1991.tb00236.x)
34. Wiernasz DC, Cole BJ. 2017 Offspring size and reproductive allocation in harvester ants. *Am. Nat.* **191**, 120–134. (doi:10.1086/694903)
35. Bulmer M. 1994 *Theoretical evolutionary ecology*. Sunderland, MA: Sinauer Associates.
36. Gocke M. 2002 Various concepts of hysteresis applied in economics. *J. Econ. Surv.* **16**, 167–188. (doi:10.1111/1467-6419.00163)
37. Alcock J. 2013 Sexual selection and the mating behavior of solitary bees. In *Advances in the study of behavior*, pp. 1–48. Oxford, UK: Elsevier Inc.
38. Izzo A, Tibbetts EA. 2015 Heightened condition dependence of a sexually selected signal in male *Polistes dominulus* paper wasps. *Ethology* **121**, 586–592. (doi:10.1111/eth.12371)
39. Holm SN. 1972 Weight and life length of hibernating bumble bee queens (Hymenoptera: Bombidae) under controlled conditions. *Ent. Scand.* **3**, 313–320. (doi:10.1163/187631272X00184)
40. Tepedino VJ, Torchio PF. 1982 Phenotypic variability in nesting success among *Osmia lignaria* propinqua females in a glasshouse environment: (Hymenoptera: Megachilidae). *Ecol. Entomol.* **7**, 453–462. (doi:10.1111/j.1365-2311.1982.tb00688.x)
41. Woodard SH, Duennes MA, Watrous KM, Jha S. 2019 Diet and nutritional status during early adult life have immediate and persistent effects on queen bumble bees. *Conserv. Physiol.* **7**, 1–10. (doi:10.1093/conphys/coz048)
42. Craig R. 1983 Subfertility and the evolution of eusociality by kin selection. *J. Theor. Biol.* **100**, 379–397. (doi:10.1016/0022-5193(83)90436-8)