



Review

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Hamilton's rule and the causes of social evolution

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Hamilton's rule is a central theorem of inclusive fitness (kin selection) theory and predicts that social behaviour evolves under specific combinations of relatedness, benefit and cost. This review provides evidence for Hamilton's rule by presenting novel syntheses of results from two kinds of study in diverse taxa, including cooperatively breeding birds and mammals and eusocial insects. These are, first, studies that empirically parametrize Hamilton's rule in natural populations and, second, comparative phylogenetic analyses of the genetic, life-history and ecological correlates of sociality. Studies parametrizing Hamilton's rule are not rare and demonstrate quantitatively that (i) altruism (net loss of direct fitness) occurs even when sociality is facultative, (ii) in most cases, altruism is under positive selection via indirect fitness benefits that exceed direct fitness costs and (iii) social behaviour commonly generates indirect benefits by enhancing the productivity or survivorship of kin. Comparative phylogenetic analyses show that cooperative breeding and eusociality are promoted by (i) high relatedness and monogamy and, potentially, by (ii) life-history factors facilitating family structure and high benefits of helping and (iii) ecological factors generating low costs of social behaviour. Overall, the focal studies strongly confirm the predictions of Hamilton's rule regarding conditions for social evolution and their causes.

1. Introduction

Hamilton's inclusive fitness theory [1,2], now 50 years old, has had a revolutionary effect on our understanding of evolution following the Modern Synthesis of the mid-twentieth century. Many works, both specialist [3–6] and more general [7–11], have explained the basis and predictions of the theory, also known as kin selection theory. Conceptually, its fundamental contribution has been to identify genes as self-promoting strategists whose evolutionary interests are conditional on the relatedness class in which they reside [1,12–14]. Put more exactly, genes are selected to act as if they are maximizing their inclusive fitness [13–15]. This insight has substantially extended population genetics, the genetical theory of natural selection and the Modern Synthesis because it shows that natural selection on any gene depends on the gene's effects, or lack of effects, on the direct fitness (offspring number) of bearers of copies of itself. Conspecific individuals are not sealed off from one another in terms of fitness, and traditional 'individual selection' is, ultimately, gene selection [12,13]. All higher levels of organization, such as genomes, multicellular organisms and societies, arise through major transitions in evolution that are conditional on cooperating genes finding a coincidence of inclusive fitness interests in bringing them about [9,13,16–19].

A simple but powerful formalization of inclusive fitness theory is provided by Hamilton's rule [20,21]. This states that a gene for any social action will undergo selection when the sum of indirect fitness (rb) and direct fitness (c) exceeds zero, where r is the relatedness of the social actor and recipient and c and b are the changes brought about by the social action in the offspring numbers of, respectively, the actor and the recipient. From Hamilton's rule follow the well-known conditions for the four possible types of social action as defined by the signs of c and b , namely cooperation or mutual benefit (+, +), altruism (–, +), selfishness (+, –) and spite (–, –) [6,7,9]. Specifically, in its most celebrated application, Hamilton's rule states that altruism (net loss of direct fitness) is selected if $rb - c > 0$. By identifying this condition, inclusive fitness theory solved the

problem of altruism [7,12]. Because of its grounding in fundamental theory, its incorporation of the four types of social action and its universal taxonomic scope, the theory provides the best current basis for a unified understanding of social evolution [5,15]. For example, it enables conflict within family groups and intragenomic conflict to be understood in the same terms [9,22]. When applied to the major transitions [9,16,17], it provides an explanation of the biological hierarchy itself.

The evidence for inclusive fitness theory is extensive, diverse and growing [8,10,11,23,24]. Nonetheless, explicit empirical tests of Hamilton's rule in natural populations are relatively few. Hamilton's rule predicts that each social action arises only under certain combinations of values of r , b and c [7,9]. Factors bringing about the required values of r , b and c within natural populations create conditions for social evolution. Variation in these values may then cause social evolution in the sense of making the difference (given appropriate genetic variation) between whether or not social behaviour undergoes selection. For example, Hamilton's rule finds that positive relatedness is a necessary condition for the evolution of altruism and that altruism evolves more readily when b is high and c is low. So, for a given relatedness structure, identifying factors affecting the relative values of b and c gives insight into the causes of altruism [21,25]. In this review, I consider results from two approaches to using Hamilton's rule and its predictions to investigate the causes of social evolution. First, I review studies that have empirically tested Hamilton's rule by estimating its parameters using genetic and demographic data from natural populations. Second, I review comparative phylogenetic analyses that have identified predicted genetic, life-history or ecological correlates of social evolution.

A consideration of studies that have tested Hamilton's rule with empirical data is worthwhile because, although several prominent studies have reported such tests, it is well known that, while measuring relatedness using molecular markers is fairly straightforward, estimating b and c in natural populations is far from easy [21]. The impression has therefore arisen that empirical tests of Hamilton's rule are vanishingly scarce and that inclusive fitness theory's successful explanation of altruism relies simply on observing positive relatedness within social groups [26,27]. As will be shown, neither of these points is correct. However, to the best of my knowledge, no previous review has aimed to collate empirical tests of Hamilton's rule and systematically analyse the insights that they provide as regards the causes of social evolution. Crespi [28] highlighted the potential power of comparative phylogenetic analyses of the correlates of sociality to identify causes of social evolution operating over evolutionary time. But many relevant studies have appeared only recently as molecular phylogenies and advances in statistical methodology have become available and, again, a synthesis of the findings of such analyses has not been carried out. Overall, I seek to consider how tests of Hamilton's rule and comparative phylogenetic analyses of the correlates of sociality advance our knowledge of the causes of social evolution at ecological and evolutionary scales.

2. Empirical tests of Hamilton's rule in natural populations

A survey of the literature for studies estimating the parameters of Hamilton's rule using genetic and demographic

data from natural populations reveals 12 studies that either have had this explicit aim or provide data permitting these parameters to be estimated (table 1 and figure 1; electronic supplementary material, table S1). The survey is not exhaustive and excludes some related studies. For example, in focusing on estimates of r , b and c , it excludes studies that test inclusive fitness theory by using empirical data to estimate inclusive fitness in other ways [42–46] or to test models of reproductive skew [47,48], which are derived from Hamilton's rule. In focusing on single species or populations, it excludes studies that test Hamilton's rule using correlations across species between social traits and relatedness, benefits or costs [49–52]. Finally, in focusing on common behaviours in natural populations, it excludes studies of rare behaviours [53] and recent applications of Hamilton's rule to social behaviour in humans [54] and robots [55]. Excluding these studies is conservative, in that most of them support the predictions of inclusive fitness theory. The lack of many more studies estimating the parameters of Hamilton's rule in natural populations shows that, indeed, benefits and costs of social actions are difficult to measure in field settings (many of the focal studies involved painstaking fieldwork over multiple years). Nonetheless, such studies are evidently not as scarce as has sometimes been suggested and, though biased towards altruistic brood-rearing behaviour, cover a broad range of other behaviours, including egg dumping, cannibalism and cooperative lekking (table 1 and figure 1; electronic supplementary material, table S1).

(a) Assumptions of empirical tests of Hamilton's rule

The studies included in the present survey (table 1 and electronic supplementary material, table S1) make a number of assumptions. First, in reaching their specific conclusions, they assume that the fitness accounting is complete, and that there are not alternative behavioural choices that occur at appreciable frequencies whose benefits and costs could not be estimated. An example of such an alternative is the behaviour within the eusocial Hymenoptera in which a subset of females enter diapause early instead of helping or nesting in the current year [46]. Fitness returns from such behaviours may, indeed, be hard to measure (in this case, because they accrue in the following year), and to this extent the relevant analyses would be incomplete. But this would be true when attempting to apply empirical data from these systems in any sort of model. Second, more generally, applying Hamilton's rule uses the 'phenotypic gambit' [21], in which it is assumed that the exact genetic basis of the focal social behaviour (which is unknown in every case) is not such as to overturn the expectations based on Hamilton's rule. The phenotypic gambit is not an assumption of the field of social evolution alone but of behavioural ecology as a whole [21], and its justification comes from behavioural ecology's outstanding success as a research programme [11]. Third, applying Hamilton's rule to data generally makes the assumptions that the social action has additive effects on fitness and that selection for the social action is weak [21,55]. When costs and benefits are estimated as offspring numbers averaged over the lifetimes of the actors and recipients, and when traits are close to equilibrium, these assumptions may be justified [3,21]. However, there are cases in which non-additivity affects the selective outcome [56,57]. Nonetheless, overall, the empirical application of Hamilton's rule is justified because it often appears robust to

Table 1. Studies parametrizing and testing Hamilton's rule with genetic and demographic data from natural populations. See electronic supplementary material, table S1 for an expanded version of the table (giving estimates of the relatedness, benefit and cost terms of Hamilton's rule in each study).

taxon/species	actor's behavioural decision	conclusion	source
1. Lace bug (<i>Gargaphia solani</i>)	female egg dumps versus not egg dumping	egg dumping is positively selected via indirect fitness benefits	[29]
2. Allodapine bee (<i>Xylocopa pubescens</i>)	usurped female guards shared nest versus leaving to nest alone	guarding is positively selected via indirect fitness benefits	[30]
3. Allodapine bee (<i>Xylocopa sulcatipes</i>)	female guards shared nest versus nesting alone	guarding was positively selected via indirect fitness benefits in one year of the study (1986) but not in the other year (1987)	[31,32]
4. Halictid bee (<i>Lasioglossum malachurum</i>)	female acts as worker versus nesting alone	worker behaviour is not positively selected via indirect fitness benefits	[33]
5. Polistine wasp (<i>Polistes annularis</i>)	female joins foundress association versus nesting alone	female joining behaviour was not positively selected at any group size in one year of the study (1977); female joining behaviour was positively selected via indirect fitness benefits at low group sizes (2–3) but not high group sizes (4 or more) in the other year (1978)	[34]
6. Polistine wasp (<i>Polistes dominulus</i>)	female joins another foundress versus nesting alone	female joining behaviour is selectively neutral	[35]
7. Polistine wasp (<i>Polistes fuscatus</i>)	female joins foundress association versus nesting alone	female joining behaviour was positively selected via indirect fitness benefits at low group size (2) but not at higher group sizes (3–9)	[36]
8. Polistine wasp (<i>Polistes metricus</i>)	female joins another foundress versus nesting alone	female joining behaviour is positively selected via indirect fitness benefits	[37]
9. Polistine wasp (<i>Ropalidia marginata</i>)	female joins foundress association versus nesting alone	female joining behaviour is positively selected via indirect fitness benefits	[38]
10. Tiger salamander (<i>Ambystoma tigrinum</i>)	larva cannibalizes non-kin versus cannibalizing kin	kin discrimination (avoidance) in cannibalistic larval salamanders is positively selected via indirect fitness benefits	[39]
11. Wild turkey (<i>Meleagris gallopavo</i>)	male cooperatively defends dominant male within male coalition in lek versus displaying singly in lek	cooperative lekking is positively selected via indirect fitness benefits	[40]
12. White-fronted bee-eater (<i>Merops bullockoides</i>)	bird acts as helper at nest of breeding pair versus dispersing and breeding	helping is positively selected via indirect fitness benefits	[41]

violations of these assumptions [55] and because it yields a valuable generality at the expense of an exactness that, in natural systems, is almost impossible to achieve [21,58]. Furthermore, applying Hamilton's rule to empirical data is particularly useful because, given it is explicitly based on fitness differences (in the b and c terms), Hamilton's rule compels investigators to analyse the central problem of why individuals exhibit one set of behaviours and not another [20,21].

(b) Conclusions from empirical tests of Hamilton's rule: forms of social behaviour and fulfilment of Hamilton's rule

Because of the interest in addressing the problem of altruism, empirical tests of Hamilton's rule have concentrated on cases

where social behaviour aids recipients at what appears, *a priori*, to be a direct fitness cost to the actor. Of the 12 focal studies (table 1 and electronic supplementary material, table S1), 10 found that actors did indeed incur a direct fitness cost (negative c) and hence exhibited altruism even though social behaviour was facultative (electronic supplementary material, table S1). In two remaining cases (egg dumping in lace bugs and kin-discriminating cannibalism in larval salamanders; nos. 1 and 10 in table 1 and electronic supplementary material, table S1), there was a direct fitness return of zero ($c = 0$). Of the 10 studies in which there was demonstrated altruism, five found that Hamilton's rule was quantitatively fulfilled, i.e. actor–recipient relatedness (r) and benefit to recipients (b) were both positive and high enough for the total indirect fitness benefit to outweigh the direct fitness cost ($-c$), such that

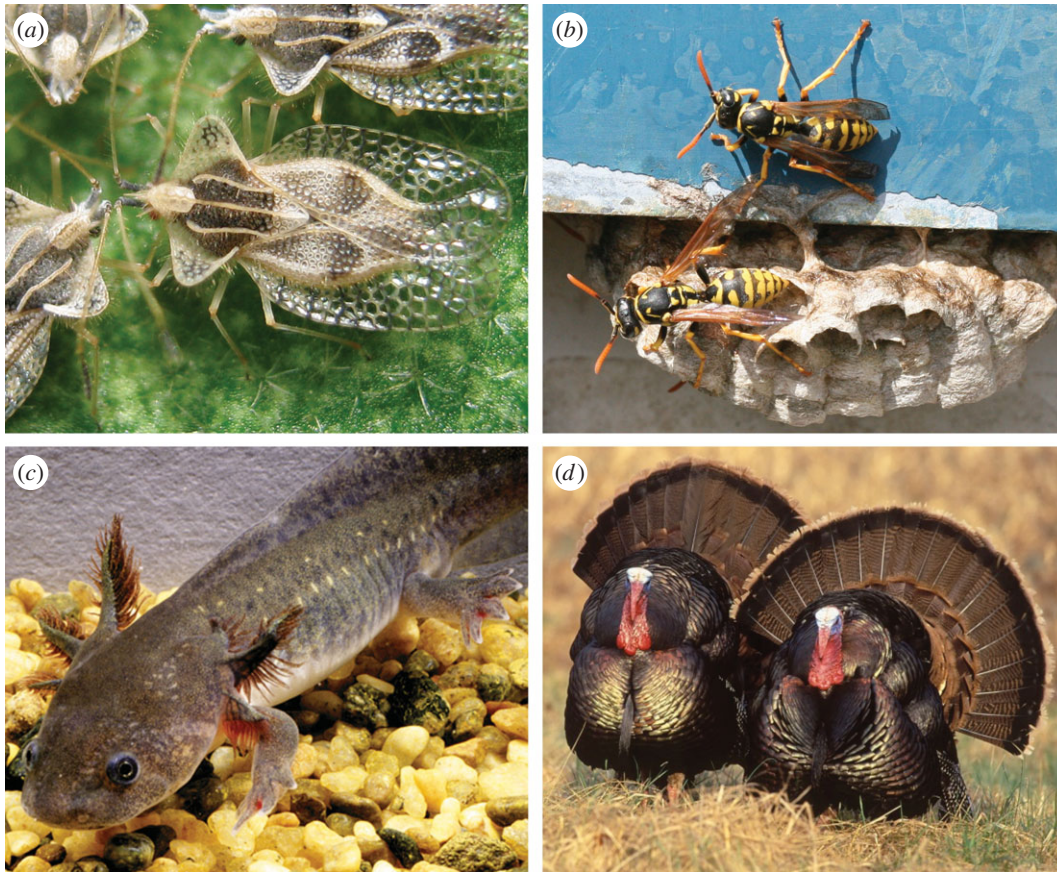


Figure 1. Hamilton's rule has been tested in a wide range contexts and organisms, including egg dumping, joining behaviour, cannibalism and cooperative lekking in, respectively (a–d): (a) Egg-plant lace bug, *Gargaphia solani* (image credit: copyright 2013 www.Croar.net); (b) Polistine wasp, *Polistes dominulus* (image credit: Andrew Bourke); (c) Tiger salamander larva, *Ambystoma tigrinum* (image credit: Kerry Matz) and (d) Wild turkey, *Meleagris gallopavo* (image credit: Tim Simos/ National Wild Turkey Federation).

$rb - c > 0$. These cases involved guarding in an allodapine bee, joining behaviour in polistine wasps, cooperative lekking in wild turkeys and helper behaviour in white-fronted bee-eaters (nos. 2, 8, 9, 11 and 12). In three cases, involving guarding in an allodapine bee and joining behaviour in polistine wasps (nos. 3, 5 and 7), Hamilton's rule was quantitatively fulfilled in some contexts (some years, some group sizes) and not others. In one case, again involving joining behaviour in a polistine wasp (no. 6), social behaviour was selectively neutral ($rb - c = 0$). In the single remaining case, involving worker behaviour in a halictid bee (no. 4), Hamilton's rule was not fulfilled ($rb - c < 0$). Overall, therefore, among 10 cases of demonstrated altruism, Hamilton's rule was quantitatively fulfilled in five cases and fulfilled in some contexts in a further three cases. Moreover, egg dumping in lace bugs and kin-discriminating cannibalism in larval salamanders (nos. 1 and 10) were each found to yield a positive indirect fitness benefit despite the lack of direct benefit (electronic supplementary material, table S1), again explaining the occurrence of these behaviours by Hamilton's rule.

(c) Conclusions from empirical tests of Hamilton's rule: relatedness

The focal studies show that there is considerable diversity in the mechanisms that generate positive actor–recipient relatedness in social systems. Standard mechanisms generating such relatedness are population viscosity (philopatry) and kin discrimination [7,9]. Population viscosity can arise through

subsociality (group formation via parent–offspring association) or, provided aggregating individuals are relatives, through semisociality (group formation via aggregation of members of the same or mixed generations) [9]. The focal studies include cases of subsociality (e.g. allodapine bee, halictid bee; nos. 3 and 4 in table 1 and electronic supplementary material, table S1), cases of semisociality of relatives (e.g. polistine wasps; nos. 5–9) and cases that probably involve a mixture of subsociality and semisociality (lace bug, allodapine bees, wild turkey, white-fronted bee-eater; nos. 1, 2, 3, 11 and 12). The focal studies also include one clear case of kin discrimination at the individual level. The study of cannibalistic larval salamanders (no. 10) suggested that kin discrimination has evolved because it allows larvae to benefit from cannibalism while avoiding harm to coexisting relatives [39]. This supports a general finding that kin discrimination evolves not as an automatic corollary of kin selection but specifically in social contexts in which it generates benefits [52,59].

(d) Conclusions from empirical tests of Hamilton's rule: benefit and cost

There are several conclusions to be drawn from the focal studies (table 1 and electronic supplementary material, table S1) as regards benefits and costs and their role in the causation of social evolution:

- (1) In cases involving cooperative breeding or eusociality, social behaviour is favoured despite its direct cost because

it yields some combination, in relatives, of increased individual or nest survivorship or increased nest productivity (allodapine bees, polistine wasps, white-fronted bee-eater; nos. 2, 3, 5, 6, 7, 8, 9 and 12 in table 1 and electronic supplementary material, table S1). In some cases, this effect can be pinned to specific advantages of larger social groups, such as the guard in an allodapine bee (no. 3) providing protection against usurpation that increases nest survivorship and providing benefits of division of labour that increase nest productivity [31,32]. Similarly, egg dumping by lace bugs and cooperative lekking in wild turkeys (nos. 1 and 11) yield indirect fitness benefits because they increase the survivorship of the brood of related recipients and the reproductive output of related, dominant males, respectively. Hence, the long-standing idea that advantages of larger group sizes relative to solitary living help generate the indirect fitness benefits that tilt the balance in favour of sociality receives detailed support from these studies.

- (2) In one eusocial insect case (halictid bee; no. 4), Hamilton's rule failed the test, because workers did not receive a sufficiently large indirect fitness benefit to offset their direct fitness cost. In this case, it was suggested that queens manipulated workers into helping [33]. However, several lines of evidence suggest that queen manipulation is not a general cause of the origin of eusociality in halictid bees or eusocial Hymenoptera as a whole [10,46,60].
- (3) Social behaviour that, in net terms, is altruistic, can nonetheless involve a mixture of indirect and direct fitness gains. For example, in an allodapine bee and at least two of the polistine wasps (nos. 2, 5 and 7), social females gained some direct fitness either through nest inheritance or through laying eggs in the joint nest. However, the size of the direct fitness benefit in these females was, as data in the original studies showed [30,34,36], insufficient to outweigh the direct fitness return from solitary nesting, such that social behaviour remained altruistic (negative c ; electronic supplementary material, table S1). In other systems, including other populations of polistine wasps, direct benefits can be sufficiently large that joining behaviour becomes cooperative (mutually beneficial) but not altruistic [45,61]. In general, each b and c term is a difference of two components (recipient's direct fitness in the presence and absence of the social action, actor's direct fitness in the presence and absence of the social action). Hence, factors affecting any one of these four components can affect the form of the social behaviour, the balance of indirect and direct returns to actors and the conditions required for social behaviour to undergo selection.
- (4) Cases in which Hamilton's rule was fulfilled in some contexts but not others (nos. 3, 5 and 7) point to possible ecological and demographic causes mediated by changes to b and c . One is annual variation in the external environment altering the relative values of the components of b and c such that sociality is disfavoured. For example, in an allodapine bee (no. 3), a year in which nest usurpations were rare appears to have increased the direct fitness return from solitary nesting (reflected in the increased c term in 1987 in the electronic supplementary material, table S1), making guarding unprofitable [31,32]. In a polistine wasp (no. 5), a drought year appears to have reduced the relative productivity of joint nests (reflected in the low b term in 1977 in the electronic supplementary material,

table S1), making joining behaviour unprofitable [34]. These results suggest that environmental variability creates temporally fluctuating selection for sociality, so accounting for the coexistence of social and solitary behaviours within populations. Another possible cause of variation affecting whether Hamilton's rule is fulfilled is suggested by two studies of polistine wasps (nos. 5 and 7), which showed that joining behaviour was positively selected at low but not at high group sizes [34,36]. In these cases, variations in the relative frequencies of groups of different size could have accounted for the variable fulfilment of Hamilton's rule.

3. Investigating the causes of social evolution using comparative phylogenetic analyses

Almost 20 comparative phylogenetic analyses, mostly conducted within the past 10 years, have allowed investigators to identify genetic, life-history and ecological correlates of the origin of sociality and so pinpoint likely causes of social evolution on an evolutionary timescale in a broad variety of social systems and taxa (table 2 and electronic supplementary material, table S2). These studies vary widely in their scale and methodology and in their ability to distinguish between the antecedents (potential causes) of sociality and its consequences; most, however, use some form of statistical comparative analysis (electronic supplementary material, table S2), lending rigour to their findings. Collectively, they provide valuable insights into the transitions that occur in social evolution and their potential causes.

(a) Genetic correlates

Hamilton's rule makes the general prediction that, other things equal, high relatedness is more conducive to forms of sociality involving altruism (cooperative breeding and eusociality) than low relatedness. In Boomsma's monogamy hypothesis [18,84,85], it makes the specific prediction that lifetime monogamy (leading to $r_{RO} = r_O$, i.e. actor's relatedness to recipient's offspring = actor's relatedness to own offspring) promotes obligate sociality. Both these predictions are borne out by the data. Multiple studies show that transitions to multicellularity (case no. 1 in table 2 and electronic supplementary material, table S2), cooperative breeding (birds and mammals; nos. 8, 9 and 11) or eusociality (shrimp, thrips and Hymenoptera; nos. 12, 15 and 18) occur preferentially under high-relatedness conditions. Boomsma's monogamy hypothesis is supported by the phylogenetic analysis of the evolution of obligate eusociality in the Hymenoptera (no. 18) and is consistent with monogamy being strongly associated with cooperative breeding in birds and mammals (nos. 8 and 9). It is also supported by the phylogenetic analysis of the evolution of obligate multicellularity (no. 1), which was found to be associated with subsociality, in that subsocial development of multicellular organisms creates conditions in which $r_{RO} = r_O$ [62]. As a corollary, all these studies confirm that, contrary to previous claims [26,86] but consistently with inclusive fitness theory, high relatedness is primary not secondary in the evolution of cooperative breeding and eusociality [8–10].

In some cases (social spiders, eusocial thrips; nos. 2 and 15), the occurrence of inbreeding contributes to the high relatedness associated with the origin of sociality, even though models show

Table 2. Comparative phylogenetic analyses of the genetic, life-history and ecological correlates of the origin of various forms of sociality. Correlates that arise as products of sociality once it has originated are not included. Conclusions are paraphrased from those of the original authors. See electronic supplementary material, table S2 for an expanded version of the table (listing identified correlates in detail).

form of sociality/taxon	conclusion	source
<i>multicellularity</i>		
1. eukaryotes and prokaryotes	group formation involving clonality (via subsociality) leads to obligate multicellularity more readily than non-clonal group formation, as predicted by inclusive fitness theory	[62]
<i>sociality without reproductive division of labour</i>		
2. spiders (Theridiidae)	sociality is promoted by extended maternal care, subsociality and inbreeding	[63]
3. primates	multi-male and female groups arise as a response to predation risk but not philopatry	[64]
<i>cooperative breeding</i>		
4. hornbills (Bucerotidae)	temporally stable environment promotes cooperative breeding	[65]
5. African starlings (Sturnidae)	temporally variable environment promotes cooperative breeding by allowing successful breeding in harsh years	[66]
6. birds (Aves)	low annual mortality predisposes lineages to cooperative breeding, and, within these lineages, sedentariness and warm, invariable climate promote cooperative breeding	[67,68]
7. birds (Aves)	warm, dry climatic conditions, together with environmental uncertainty (in rainfall), promote cooperative breeding in passerines	[69]
8. birds (Aves)	high within-group relatedness (low promiscuity) promotes cooperative breeding	[59]
9. mammals (Mammalia)	high within-group relatedness (monogamy) promotes cooperative breeding	[70]
10. mammals (Mammalia)	opportunity for helpers to increase the direct fitness of breeders is greatest in species with litters and promotes cooperative breeding	[71]
11. mammals (Mammalia)	allomaternal care is associated with indirect fitness benefits via aid to kin	[72]
<i>eusociality</i>		
12. sponge-dwelling shrimp (<i>Synalpheus</i>)	high within-group relatedness (subsociability) promotes eusociality	[73]
13. aphids (<i>Pemphigus</i>)	selection for defence against predation promotes eusociality	[74]
14. aphids (<i>Pemphigus</i>)	maximum within-group relatedness does not predict eusocial evolution in aphids but galls may nonetheless promote eusociality by generating structured populations	[75]
15. thrips (<i>Kladothrips</i> , <i>Oncothrips</i>)	high relatedness (arising partly from inbreeding) promotes eusociality	[76,77]
16. termites (Isoptera)	external foraging promotes worker evolution	[78,79]
17. wasps (Vespidae)	nesting, oviposition into an empty cell and progressive provisioning promote eusociality by permitting females to choose egg sex independently of provision mass and to interact with larvae and other adults	[80]
18. ants, bees and wasps (Hymenoptera)	high within-group relatedness (monogamy) promotes both the origin of eusociality and the origin of obligate eusociality	[81]
19. African mole-rats (Bathergidae)	food patchiness, aridity and environmental uncertainty (in rainfall) promote sociality	[82,83]

that inbreeding does not always affect relatedness in ways conducive to social evolution [87]. In social spiders, phylogenetic analysis showed that inbred, social lineages originate frequently but also go extinct frequently [63], demonstrating that sociality is not always successful on an evolutionary timescale. Eusocial aphids have intrinsic high relatedness in that colonies are founded subsocially by a single clonally reproducing female. Contrary to expectation based on Hamilton's rule, clonal mixing was found to be present in, and ancestral to, eusocial and non-eusocial *Pemphigus* aphids (no. 14). Nonetheless, within-group relatedness remains high within galls of eusocial

aphids [9,75], and the association of aphid eusociality with galling suggests that population structure imposed by galling is a contributory factor in the group's social evolution [75].

(b) Life-history correlates

Queller & Strassmann [88] divided eusocial species into 'fortress defenders' (species that live within a defended food source) and 'life insurers' (species with external foragers whose reproductive investments are safeguarded by nest-mates). These concepts, which stress the long-standing idea

that nesting acts as a key life-history facilitator of social evolution [9], receive support from the focal studies. Hence, the appearance of nesting is basal to the appearance of eusociality within vespoid wasps [80] and, in termites, the switch to external foraging is associated with the origin of sterile workers [78,79] (case nos. 16 and 17 in table 2 and electronic supplementary material, table S2). Arnold & Owens [67,68] introduced the concept of life-history predisposition followed by ecological facilitation, according to which life-history traits predispose lineages to sociality but ecological factors determine whether it evolves or not. This concept also receives support in that several studies identify life-history traits preceding the origin of sociality, including extended maternal care (social spiders; no. 2), increased adult longevity (birds; no. 6), litter-bearing (mammals; no. 10) and control over egg sex and interactions with larvae (eusocial Hymenoptera; no. 17). However, the finding in birds that adult longevity is positively associated with the transition to cooperative breeding has been disputed on methodological grounds ([89]; electronic supplementary material, table S2). In mammals, cooperative breeding was not found to be associated with adult longevity (no. 10). Several of the identified traits facilitate social evolution according to Hamilton's rule, because nesting, subsociality and (if present) extended longevity promote close, predictable family structure (high, consistent r) and litter-bearing facilitates the generation of large benefits by helping behaviour (high b).

(c) Ecological correlates

The focal studies indirectly identify predation risk as an ecological factor promoting sociality in primates and eusocial aphids (nos. 3 and 13 in table 2 and electronic supplementary material, table S2). This is consistent with the expectation from Hamilton's rule that low direct fitness returns from breeding alone (leading to low c) promote social behaviour. In birds, results of the focal studies are mixed as regards the influence of environmental variation [65–69]. Although methodological differences may explain some discrepancies (electronic supplementary material, table S2), available evidence suggests that non-passerine and passerine birds differ in their response to environmental variation. Specifically, cooperative breeding is positively associated with climatically stable environments in hornbills and non-passerine birds as a group (nos. 4 and 7) and with warm, climatically variable environments in African starlings and passerine birds as a group (nos. 5 and 7). Why non-passerines and passerines differ in this respect is not resolved, but differences between the groups in body size, territoriality and diet may be partly responsible [65,69]. From Hamilton's rule, one might predict harsh variable environments to promote cooperative breeding in passerine birds through decreasing direct fitness returns from breeding alone [66]. In non-passerine birds, one might predict stable environments to promote cooperative breeding indirectly if, because of traits of non-passerine birds, they increased adult survival and longevity and so decreased the number of territory vacancies. The resulting habitat saturation would again decrease direct fitness returns from breeding alone [65]. These interpretations predict that non-passerine and passerine birds differ in how their intrinsic traits interact with environmental factors with respect to the evolution of cooperative breeding, and hence require further studies for support or refutation. Finally, warm, dry, environmentally variable conditions were associated with sociality in African mole-rats (no. 19), once more

suggesting, consistent with Hamilton's rule, that low direct fitness returns from solitary breeding promote cooperative behaviour.

4. Discussion

Overall, the studies considered in this review strongly confirm the predictions of Hamilton's rule regarding the conditions and likely causes that underpin social evolution at ecological and evolutionary timescales. Studies parametrizing Hamilton's rule with data from natural populations are not rare and demonstrate quantitatively that (i) altruism occurs even when sociality is facultative, (ii) in most cases, altruism is under positive selection via indirect fitness benefits that exceed direct fitness costs and (iii) social behaviour commonly generates indirect benefits by enhancing the productivity or survivorship of kin. The studies also provide evidence for environmental variability altering the direction of selection on social behaviour by changing the relative values of benefits and costs. Comparative phylogenetic analyses of the correlates of sociality show that cooperative breeding and eusociality are promoted by (i) high relatedness and monogamy and suggest that they are also promoted by (ii) life-history factors facilitating family structure and high benefits of helping and (iii) ecological factors generating low costs of social behaviour. Variations on these patterns, exceptions and unresolved discrepancies exist, especially as regards identifying, in comparative phylogenetic analyses, correlates of sociality that accurately reflect benefits and costs. Equally, Hamilton's rule is upheld in novel contexts such as egg dumping, cannibalism and cooperative lekking. Collectively, the focal studies provide strong, additional formal evidence for the predictions of inclusive fitness theory.

These findings also suggest promising avenues for future progress. First, in highlighting the general applicability of inclusive fitness theory, they suggest that extensions to additional taxa and contexts will be similarly fruitful. For example, although group formation in multicellularity follows predictions of the theory (table 2), studies estimating the empirical parameters of Hamilton's rule as it applies to the origin of multicellularity within single populations of cells remain to be performed, though several candidate systems exist [9,90]. Second, they suggest that Hamilton's rule for social actions other than altruism, such as spite, could be profitably tested by empirical parametrization [91]. Future empirical parametrizations might also benefit from incorporating more sophisticated methods of fitness accounting [92], or from quantifying effects of other social phenomena that can affect inclusive fitness returns such as sex ratio variation [60], reproductive skew [47] and kin competition [51]. Third, the predictive power of empirical parametrizations of Hamilton's rule could be improved in other ways. For example, in facultatively eusocial Hymenoptera, it remains to be shown (which would be challenging, but not impossible) that social behaviour increases in frequency under conditions in which Hamilton's rule is fulfilled and decreases in frequency under conditions in which it is not fulfilled.

Fourth, causation ultimately requires experimental demonstration, and the focal studies provide strong indicators of likely causes of social evolution that could inform experiments. Indeed, several studies, for example, in insects [48,93] and microbes [94,95], have already successfully tested inclusive fitness theory by experimentally varying

the parameters of Hamilton's rule. Finally, phylogenomic and transcriptomic studies are now beginning to uncover some of the specific genes likely to be important in the origin and maintenance of sociality [96,97]. A combination of strong basic theory, applications to new contexts, additional comparative analyses, carefully targeted experimental manipulations and knowledge of genetic underpinnings

will prove extremely potent in accelerating the future growth of our understanding of social evolution.

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