Hamilton's rule and the causes of social evolution - electronic supplementary material

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Notes to Table S2

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Table S1. Studies parametrizing and testing Hamilton's rule with genetic and demographic data from natural populations. Relatedness was measured using allozyme or microsatellite analysis or was inferred from pedigrees. $r_O =$ actor's relatedness to its own offspring; $r_R$, actor's relatedness to the recipient; $r_{RO} =$ actor's relatedness to the recipient's offspring; $b$, change in direct fitness (offspring number) of recipient; $c$, change in direct fitness of actor. Hamilton's rule is used in two main forms: the first ($r_Rb + c > 0$) weights the indirect fitness term by the actor's relatedness to the recipient and the second ($r_{RO}b + r_Oc > 0$) weights the indirect fitness term by the actor's relatedness to the recipient's offspring and the direct fitness term by the actor's relatedness to its own offspring. Both forms sum the indirect and direct fitness terms when (as here) $c$ is defined as being positive (if the actor experiences a net gain in direct fitness) or negative (if the actor experiences a net loss in direct fitness, i.e. altruism). The method of calculation and form of Hamilton's rule employed here differ in some cases from those of the original authors, but all major conclusions remain the same.

<table>
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<th>Taxon/species</th>
<th>Actor's behavioural decision</th>
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<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Lace bug (Gargaphia solani)</td>
<td>Female egg dumps versus not egg dumping</td>
<td>$r_R = 0.362$ \ $b = 13.61$, $c = 0.607$</td>
<td>$r_Rb + c &gt; 0$; \ $(0.362)(13.61) + (0.607)^a$ = 5.53</td>
<td>Egg dumping is positively selected via indirect fitness benefits. Egg dumping returns an indirect fitness benefit because it increases the survivorship of recipients' broods, and egg dumpers and recipients are related on average. Egg dumping does not return a direct fitness benefit to egg dumpers ($c$ was not significantly different from zero).</td>
<td>[1]</td>
</tr>
<tr>
<td>2. Allodapine bee (Xylocopa pubescens)</td>
<td>Usurped female guards shared nest versus leaving to nest alone</td>
<td>$r_{RO} = 0.208$, $r_O = 0.5$ \ $b = 2.02$, $c = -0.327^b$</td>
<td>$r_{RO}b + r_Oc &gt; 0$; \ $(0.208)(2.02) - (0.5)(0.327) = 0.257$</td>
<td>Guarding is positively selected via indirect fitness benefits. Guarding returns an indirect fitness benefit because guarding increases nest productivity and usurped females remain as guards more often when usurped</td>
<td>[2]</td>
</tr>
</tbody>
</table>
by nestmates, to which they are related on average. Guarding incurs a direct fitness cost because, although guards achieve some direct fitness from nest inheritance, this does not outweigh the direct fitness benefit guards can achieve by nesting alone.

| 3. Allodapine bee (Xylocopa sulcatipes) | Female guards shared nest versus nesting alone | 1986: Daughter guards for mother: $r_{RO} = 0.5$, $r_O = 0.5$

$b = 4.02$, $c = -1.46$

Sister guards for sister: $r_{RO} = 0.375$, $r_O = 0.5$

$b = 3.24$, $c = -1.46$

Female guards for alien female$^c$: $r_{RO} = 0.25$, $r_O = 0.5$

$b = 4.64$, $c = -1.46$

1987: Daughter guards for mother: $r_{RO} = 0.5$, $r_O = 0.5$

$b = 1.00$, $c = -4.57$

Sister guards for sister: $r_{RO} = 0.375$, $r_O = 0.5$

$b = 0.13$, $c = -4.57$

Female guards for alien female$^c$: $r_{RO} = 0.25$, $r_O = 0.5$

$b = 2.43$, $c = -4.57$

$R_{RO}b + r_Oc > 0$;

1986: Daughter guards for mother: $(0.5)(4.02)-(0.5)(1.46) = 1.28$

Sister guards for sister: $(0.375)(3.24)-(0.5)(1.46) = 0.485$

Female guards for alien female: $(0.25)(4.64)-(0.5)(1.46) = 0.43$

1987: Daughter guards for mother: $(0.5)(1.00)-(0.5)(4.57) = -1.785$

Sister guards for sister: $(0.375)(0.13)-(0.5)(4.57) = -2.236$

Female guards for alien female: $(0.25)(2.43)-(0.5)(4.57) = -1.677$

Guarding was positively selected via indirect fitness benefits in one year of the study (1986) but not in the other year (1987). Guarding returns an indirect fitness benefit because it protects against usurpation and increases the productivity of nests and guards and dominant females are related on average. Guarding incurs a direct fitness cost because all guards' eggs are eaten by the dominant female. In 1987 guarding was not positively selected because both survivorship and productivity of singletons were higher in that year, decreasing the benefit and increasing the cost of guarding. | 3, 4 |

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| 4. Halictid bee  
(Lasioglossum malachurum) | Female acts as worker versus nesting alone | First brood worker:  
\( r_R = 0.5, r_O = 0.5 \)  
\( b = 1.08, c = -3.5 \)  
Second brood worker:  
\( r_R = 0.5, r_O = 0.5 \)  
\( b = 1.08, c = -1.4 \) | \( r_R b + r_O c > 0; \)  
First brood worker:  
\( (0.5)(1.08)-(0.5)(3.5) = -1.21 \)  
Second brood worker:  
\( (0.5)(1.08)-(0.5)(1.4) = -0.16 \) | Worker behaviour is not positively selected via indirect fitness benefits. Worker behaviour returns an indirect fitness benefit, as workers rear their mother queen's offspring. Worker behaviour incurs a direct fitness cost because workers lose offspring by not nesting alone. This fitness cost outweighed the indirect benefit of working. The authors suggest that manipulation by queens maintains worker behaviour in this system. | [5] |
| 5. Polistine wasp  
(Polistes annularis) | Female joins foundress association versus nesting alone | 1977:
Total group size = 2:  
\( r_R = 0.498 \)  
\( b = -1.331, c = -3.409 \)  
Total group size = 3:  
\( r_R = 0.498 \)  
\( b = 1.363, c = -3.053 \)  
Total group size = 4:  
\( r_R = 0.498 \)  
\( b = 2.365, c = -2.668 \)  
Total group size = 5–6:  
\( r_R = 0.498 \)  
\( b = 1.156, c = -2.835 \) | \( r_R b + c > 0; \)  
1977:
Total group size = 2:  
\( (0.498)(-1.331)-(3.409) = -4.072 \)  
Total group size = 3:  
\( (0.498)(1.363)(3.053) = -2.374 \)  
Total group size = 4:  
\( (0.498)(2.365)-(2.668) = -1.490 \)  
Total group size = 5–6:  
\( (0.498)(1.156)-(2.835) = -2.259 \)  
Total group size = 7+:  
\( (0.498)(0.665)-(2.877) = -2.546 \) | 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). Joining behaviour generally returns an indirect fitness benefit because it increases the dominant female's productivity and foundresses are related on average. Joining behaviour always incurs a direct fitness cost because singletons produce | [6] |
### 6. Polistine wasp (Polistes dominulus)

<table>
<thead>
<tr>
<th>Group Size</th>
<th>Formula</th>
</tr>
</thead>
</table>
| Total group size = 7+:                      | \[ r_R = 0.498 \]
|                     | \[ b = 0.665, c = -2.877 \]                                           |
| 1978: Total group size = 2:                 | \[ r_R = 0.537 \]
|                     | \[ b = 38.488, c = -1.118 \]                                           |
| Total group size = 3:                        | \[ r_R = 0.537 \]
|                     | \[ b = 13.019, c = -2.214 \]                                           |
| Total group size = 4:                        | \[ r_R = 0.537 \]
|                     | \[ b = 3.883, c = -3.480 \]                                            |
| Total group size = 5–6:                      | \[ r_R = 0.537 \]
|                     | \[ b = 2.401, c = -3.554 \]                                            |
| Total group size = 7+:                        | \[ r_R = 0.537 \]
|                     | \[ b = 2.600, c = -2.881 \]                                            |

#### Female joins another foundress versus nesting alone

- \[ k = \text{ratio of productivities of 2-foundress versus 1-foundress nests} \]
- \[ z = \text{probability of 1-foundress nest survivorship} \]
- \[ r_R = 0.65 \]
- \[ k = 1.52 \]
- \[ z = 0.36 \]

\[ r_R (k - (1 + \ln z)) - 1 > 0^c; \]
\[ (0.65)(1.52 - (1 - 1.022)) - 1 = 0.002 \]

**Notes:**

The authors suggest that joining females were constrained to join by nest-site shortages (which would reduce \( c \)). A drought in 1977 may have led to low productivity of nests at all group sizes.
because single-foundress nests have reduced survivorship. In the study population, these two components of inclusive fitness balance one another out almost exactly.

| 7. Polistine wasp (Polistes fuscatus) | Female joins foundress association versus nesting alone | Total group size = 2:  
$r_R = 0.57$  
$b = 22.133$, $c = -12.233$  
Total group size = 3:  
$r_R = 0.57$  
$b = 4.704$, $c = -14.129$  
Total group size = 4:  
$r_R = 0.57$  
$b = 0.712$, $c = -15.212$  
Total group size = 5–9:  
$r_R = 0.57$  
$b = 0.420$, $c = -15.124$ | $r_R b + c > 0$;  
Total group size = 2:  
$(0.57)(22.133)-(12.233) = 0.383$  
Total group size = 3:  
$(0.57)(4.704)-(14.129) = -11.448$  
Total group size = 4:  
$(0.57)(0.712)-(15.212) = -14.806$  
Total group size = 5–9:  
$(0.57)(0.420)-(15.124) = -14.885$ | Female joining behaviour was positively selected via indirect fitness benefits at low group size (2) but not at higher group sizes (3–9). Joining behaviour returns an indirect fitness benefit because it increases the dominant female's productivity and foundresses are related on average. Joining behaviour always incurs a direct fitness cost because singletons produce more offspring than subordinate joiners. Above a group size of 2, the direct fitness cost outweighs the indirect fitness benefit. [8] |

| 8. Polistine wasp (Polistes metricus) | Female joins another foundress versus nesting alone | $r_R = 0.63$  
$b = 2.105$, $c = -1.000$ | $r_R b + c > 0$;  
$(0.63)(2.105) – 1.000 = 0.326$ | Female joining behaviour is positively selected via indirect fitness benefits. Joining behaviour returns an indirect fitness benefit because it increases nest productivity and survivorship and foundresses are related on average. Joining behaviour incurs a direct fitness cost because single-foundress |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th>Female joins foundress association versus nesting alone</th>
<th>( r_{RO} = 0.20, \ r_{O} = 0.5 ) ( b = 5.289, \ c = -0.184 )</th>
<th>( r_{RO}b + r_{O}c &gt; 0 ); ( (0.20)(5.289)-(0.5)(0.184) = 0.966 )</th>
<th>Female joining behaviour is positively selected via indirect fitness benefits. Joining behaviour returns an indirect fitness benefit because it increases joiners’ survivorship and joiners are related to the brood they rear, on average. Joining behaviour incurs a direct fitness cost because single-foundresses have reduced survivorship.</th>
</tr>
</thead>
<tbody>
<tr>
<td>9. Polistine wasp (<em>Ropalidia marginata</em>)</td>
<td></td>
<td></td>
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<tr>
<td>10. Tiger salamander (<em>Ambystoma tigrinum</em>)</td>
<td></td>
<td>Larva cannibalizes non-kin versus cannibalizing kin</td>
<td>( r_{R} = 0.5 ) ( b = 2.0, \ c = 0 )</td>
<td>( r_{R}b + c &gt; 0 ); ( (0.5)(2.0) – 0 = 1.0 )</td>
<td>Kin discrimination (avoidance) in cannibalistic larval salamanders is positively selected via indirect fitness benefits. Kin avoidance returns an indirect fitness benefit because it leads to more siblings surviving within broods. It does not incur a direct fitness cost (kin- and non-kin-discriminating larvae did not differ significantly in survivorship, growth rate or age at metamorphosis).</td>
</tr>
<tr>
<td>11. Wild turkey (<em>Meleagris gallopavo</em>)</td>
<td></td>
<td>Male cooperatively defends dominant male within</td>
<td>( r_{R} = 0.42 ) ( b = 6.1, \ c = -0.9 )</td>
<td>( r_{R}b + c &gt; 0 ); ( (0.42)(6.1) – 0.9 = 1.7 )</td>
<td>Cooperative lekking is positively selected via indirect fitness benefits. Cooperative lekking returns an indirect fitness benefit because dominant males within</td>
</tr>
</tbody>
</table>
male coalition in lek versus displaying singly in lek | coalitions gain additional mates and so father additional offspring, and they are related to subordinates males on average. Cooperative lekking incurs a direct fitness cost because subordinate males within coalitions father no offspring.

| 12. White-fronted Bee-eater (*Merops bullockoides*) | Bird acts as helper at nest of breeding pair versus dispersing and breeding | \(r_{BO} = 0.33, r_{O} = 0.5 \) \( b = 0.472, c = -0.168 \) | \( r_{BO}b + r_{O}c > 0; (0.33)(0.472)-(0.5)(0.168) = 0.072 \)

Helping is positively selected via indirect fitness benefit because it increases a pair's number of fledged young, to which helpers are related on average. Helping incurs a direct fitness cost because helpers could have more young by dispersing and breeding. | [13] |
Notes to Table S1

\(^a\)This is the more conservative parametrization of Hamilton's rule (Model A) in the original study [1].

\(^b\)The value of \(c\) has been recalculated from data in the original study [2] on differences between guards' direct fitness as guards and as single nesters.

\(^c\)In this case, a relatedness of 0.25 was assumed in the original study [3].

\(^d\)The values of \(b\) and \(c\) have been calculated according to the version of Hamilton's rule modified for group size effects derived in the original study [6].

\(^e\)This form of Hamilton's rule is taken from the original study [7].

\(^f\)The data have been reanalysed here using the modified Hamilton's rule in [6] and the relatedness value from [14]. Grafen [15] published a reanalysis of the same data.

\(^g\)The analysis method differs from that of the original study [9]; \(b\) and \(c\) are expressed in relative terms.

\(^h\)The values of \(r_{RO}\), \(b\) and \(c\) used here are the most conservative from within the ranges estimated in the original study [10], i.e. the least conducive to Hamilton's rule being fulfilled.

\(^i\)The value for \(b\) is a minimum value according to the data in the original study [11].
Table S2. 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.

<table>
<thead>
<tr>
<th>Form of sociality/taxon</th>
<th>Finding</th>
<th>Conclusion</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Multicellularity</strong>⁸:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Eukaryotes and prokaryotes</td>
<td>Taxa with subsocial cell aggregation are significantly more likely to make the transition to obligate multicellularity than taxa with semisocial cell aggregation.</td>
<td>Group formation involving clonality (via subsociality) leads to obligate multicellularity more readily than non-clonal group formation, as predicted by inclusive fitness theory.</td>
<td>[16]</td>
</tr>
<tr>
<td><strong>Sociality without reproductive division of labour:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Spiders (Theridiidae)</td>
<td>Sociality is significantly associated with extended maternal care. Sociality is concentrated in lineages with inbreeding and female-biased sex ratios.</td>
<td>Sociality is promoted by extended maternal care, subsociality and inbreeding.</td>
<td>[17]</td>
</tr>
<tr>
<td>3. Primates</td>
<td>Transition from solitary behaviour to multi-male and female groups is significantly associated with transition from nocturnal to diurnal activity patterns. Stable social groups with natal philopatry or stable pair-bond arise from multi-male and female groups.</td>
<td>Multi-male and female groups arise as a response to predation risk but not philopatry.</td>
<td>[18]</td>
</tr>
<tr>
<td><strong>Cooperative breeding:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Hornbills (Bucerotidae)</td>
<td>Cooperative breeding is significantly associated with reduced within-year variation in temperature and rainfall and with reduced between-year variation in rainfall.</td>
<td>Temporally stable environment promotes cooperative breeding.</td>
<td>[19]</td>
</tr>
<tr>
<td>5. African starlings (Sturnidae)</td>
<td>Cooperative breeding is significantly associated with semi-arid savannah habitats and with temporal variability in rainfall.</td>
<td>Temporally variable environment promotes cooperative breeding by allowing successful breeding in harsh years.</td>
<td>[20]</td>
</tr>
<tr>
<td>6. Birds (Aves)</td>
<td>Cooperative breeding is significantly associated with Low annual mortality predisposes lineages to</td>
<td></td>
<td>[21, 22]</td>
</tr>
</tbody>
</table>

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<p>| 7. Birds (Aves) | Cooperative breeding is significantly associated with higher mean temperature in passerines and non-passerines, with lower mean rainfall in passerines but not in non-passerines and with between-year variation in rainfall in passerines but not in non-passerines. | Warm, dry climatic conditions, together with environmental uncertainty (in rainfall), promote cooperative breeding in passerines. |
| 8. Birds (Aves) | Transitions to cooperative breeding are significantly associated with low promiscuity. | High within-group relatedness (low promiscuity) promotes cooperative breeding. |
| 9. Mammals (Mammalia) | Transitions to cooperative breeding are significantly associated with social monogamy. | High within-group relatedness (monogamy) promotes cooperative breeding. |
| 10. Mammals (Mammalia) | Cooperative breeding is significantly associated with bearing of multiple offspring per birth but not with adult longevity. | Opportunity for helpers to increase the direct fitness of breeders is greatest in species with litters and promotes cooperative breeding. |
| 11. Mammals (Mammalia) | Allomaternal care within groups is significantly associated with increased relatedness. | Allomaternal care is associated with indirect fitness benefits via aid to kin. |
| <strong>Eusociality:</strong> | | |
| 12. Sponge-dwelling shrimp (Synalpheus) | Eusociality is significantly associated with crawling, non-dispersing larvae (subsociality). | High within-group relatedness (subsociality) promotes eusociality. |
| 13. Aphids (Pemphigus) | Eusociality (with sterile soldiers) is associated with a long-lived gall. | Selection for defence against predation promotes eusociality. |
| 14. Aphids (Pemphigus) | The origin of eusociality is preceded by the evolution of clonal mixing, which is ubiquitous. | Maximum within-group relatedness does not predict eusocial evolution in aphids but galls may nonetheless promote eusociality by generating structured populations. |</p>
<table>
<thead>
<tr>
<th>15. Thrips (Kladothrips, Oncothrips)</th>
<th>The origin of eusociality is associated with high relatedness arising partly from inbreeding.</th>
<th>High relatedness (arising partly from inbreeding) promotes eusociality.</th>
<th>[31, 32]</th>
</tr>
</thead>
<tbody>
<tr>
<td>16. Termites (Isoptera)</td>
<td>Independent origins of 'true workers' (sterile workers) appear associated with a move to foraging outside the nest (from 'one-piece' to 'separate-piece' nesting).</td>
<td>External foraging promotes worker evolution.</td>
<td>[33, 34]</td>
</tr>
<tr>
<td>17. Wasps (Vespidae)</td>
<td>The origin of vespid eusociality is associated with the origin of nesting, oviposition into an empty cell and progressive provisioning of larvae.</td>
<td>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.</td>
<td>[35]</td>
</tr>
<tr>
<td>18. Ants, bees and wasps (Hymenoptera)</td>
<td>Independent origins of eusociality are significantly associated with ancestral monandry (single mating by female) and monogyny (one reproductive female per nest); high levels of polyandry arose after workers lost their ability to mate.</td>
<td>High within-group relatedness (monogamy) promotes both the origin of eusociality and the origin of obligate eusociality.</td>
<td>[36]</td>
</tr>
<tr>
<td>19. African mole-rats (Bathyergidae)</td>
<td>Group size is significantly negatively associated with tuber density and rainfall and significantly positively associated with variability in rainfall.</td>
<td>Food patchiness, aridity and environmental uncertainty (in rainfall) promote sociality.</td>
<td>[37, 38]</td>
</tr>
</tbody>
</table>
Notes to Table S2

a Multicellularity is included as a form of sociality (of cells) as envisaged by the major transitions approach to social evolution [39, 40].

Arnold and Owens [21, 22] found low annual mortality to be significantly associated with cooperative breeding in birds, but Cockburn [41] argued that this result could have stemmed, in oscine passerines, from the relative scarcity of adult mortality data in pair-breeding species from the tropics or the southern hemisphere, some of which appear long-lived.

Arnold and Owens [21, 22] also found warm, invariable climates to be significantly associated with cooperative breeding in birds, whereas the later study by Jetz and Rubenstein [23] found across-year variation in rainfall to be the strongest correlate. Reasons for this discrepancy are not fully clear. Jetz and Rubenstein [23] suggested that their separation of environmental variation into the three components, mean, within-year variation and among-year variation, allowed a more fine-grained analysis. Possible biological reasons, stemming from differences between non-passerines and passerines in their responses to environmental variation with respect to the evolution of cooperative breeding, are discussed in the main text.
References for electronic supplementary material


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Cornwallis CK, West SA, Davis KE, Griffin AS. 2010 Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969-972.


