BRIEF COMMUNICATIONS

Enforced altruism in insect societies

Cooperation among workers and their seeming altruism result from strict policing by nestmates.

Workers of many species of ant, bee and wasp do not lay eggs, despite having functional ovaries[1], but the selective causes of this extreme form of altruism are unclear[2–7]. Here we show that workers forego reproduction in response to the threat of their eggs being killed, or 'policed', by nestmates. Our results indicate that social coercion helps to explain worker altruism and cooperation in modern-day insect societies[3–5].

Why, in some species, do most workers forego direct reproduction? One possibility is that worker altruism is voluntary: in this scenario, high genetic relatedness should drive the evolution of altruism[2–7] and worker sterility[7] because higher relatedness increases the indirect benefit of working. Theoretically, however, worker altruism could also be 'enforced' and may have evolved in response to social sanctions[4–6]. In many species, worker-laid eggs are killed by the queen or by other workers[1,8,9] and, if these sanctions are effective, the advantage to workers of laying eggs is reduced. As a result, more would be selected to work altruistically, rather than to lay eggs[6].

The role of sanctions in promoting worker sterility has long been suspected[8,9], but has never been tested in a comparative study. We therefore studied ten single-queen species, nine Vespidae wasps (for example, see Fig.1) and the honey-

Figure 1 | **The wasp *Vespa crabro*.**

bee *Apis mellifera*. These are the only species for which there are data to quantify both the proportion of non-egg-laying workers, a measure of worker altruism, and two key predictor variables: relatedness among workers, which depends on the frequency of queen mating, and the effectiveness with which worker-laid eggs are policed by nestmates[1,8,9]. We analysed the data by using individual species as data points and by phylogenetically independent contrasts (PICs) to control for phylogenetic non-independence. (See supplementary information.)

Figure 2 shows that, as predicted, fewer workers reproduce when the effectiveness of policing worker-laid eggs is higher ($P = 0.00004$, Fig. 2a; using PICs: $P = 0.000006$, see supplementary information). This supports the hypothesis that worker altruism is enforced. Contrary to the voluntary-altruism hypothesis[7], however, higher relatedness does not lead to increased altruism. In fact, the reverse is true — a larger proportion of the workers reproduce in species where relatedness is high ($P = 0.004$, Fig. 2b; using PICs: $P = 0.04$; see supplementary information). However, this is predicted by policing theory, because low relatedness more strongly selects for workers to police each others' reproduction[1,8].

Our results also show that policing effective-

Figure 2 | **Effect of sanctions and relatedness on worker altruism in social insects. a**, If altruism is enforced, more workers should remain sterile when their reproduction is more effectively policed by nestmates, which is what occurs ($R = -0.94$, $P = 0.00004$; effectiveness of policing is reverse $\log_{10}$-transformed). **b**, If altruism is voluntary, greater altruism and less worker reproduction should be seen when relatedness is high, but the opposite occurs ($R = 0.82$, $P = 0.004$; percentage of reproductive workers is $\log_{10}$-transformed). The effectiveness of policing is defined as the probability of worker-laid eggs being killed relative to queen-laid eggs; reproductive workers are shown as the percentage of workers with active ovaries (see supplementary information).

ness is negatively correlated with relatedness ($R = -0.60$, one-tailed $P = 0.03$; using PICs: $F(1,8) = 4.69$, one-tailed $P = 0.03$); this contrasts with our results from queenless colonies, in which the relationship is reversed and higher relatedness results in a smaller proportion of the workers laying eggs ($R = -0.79$, $P = 0.007$; using PICs: $P = 0.03$; see supplementary information). This is as expected from theory, as in queenless colonies policing does not occur and its inhibitory effect is lost[7]. However, the effect of relatedness in promoting altruism remains[7].

The key role of relatedness in the evolution of self-sacrificing behaviour is widely recognized[2,5]. The origin of insect societies is one of the most cited examples, and high relatedness was probably required for worker behaviour first to evolve[2,5]. Nevertheless, our results show that in modern-day insect societies it is mainly social sanctions that reduce the numbers of workers that act selfishly. In this, they provide evidence for something that has proved notoriously hard to demonstrate in human society: that better law enforcement can lead to fewer individuals behaving antisocially[10].

Tom Wenseleers*†, Francis L. W. Ratnieks*‡
*Institute for Advanced Study, 14193 Berlin, Germany
†Present addresses: Zoological Institute, Catholic University of Leuven, 3000 Leuven, Belgium (T.W.); Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK (F.L.W.R.)
e-mail: tom.wenseleers@bio.kuleuven.be

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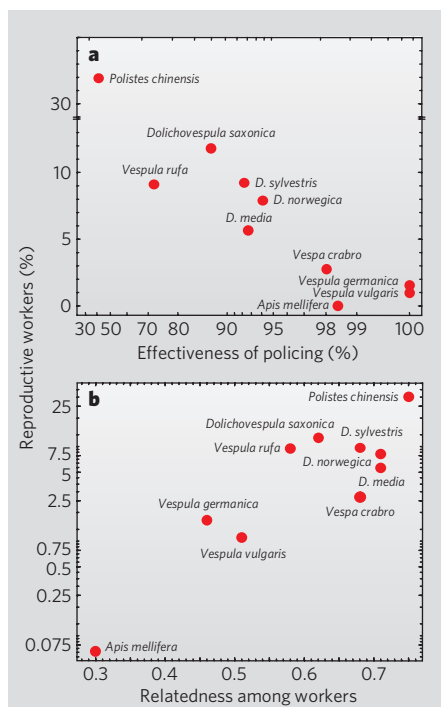10. Levitt, S. D. *Am. Econ. Rev.* **87,** 270–290 (1997).

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Supplementary Methods

Data collection. Data on relatedness, the effectiveness of policing, and the percentage of egg-laying workers were collected from 10 single-queen species, 9 Vespidae wasps and the honeybee *Apis mellifera*, and came largely from our own published studies (Fig. S1, Tables S1-S3). Relatedness values were taken from references 1-7. Policing effectiveness was estimated as described in the section below. The proportions of reproductive workers in colonies with and without a queen were determined using dissection and came from references 3-14 and Wenseleers, unpublished data (Table S1). A worker was classified as reproductive when the largest oocyte in her ovaries was at least 50% the size of a mature egg. To exclude the possibility that workers in species with pronounced queen-worker dimorphism are less capable of reproducing, we also obtained estimates of queen-worker dimorphism based on the ratio of the body lengths of queens and workers, measured for 10 individuals per caste per species (Fig. S1). For *Polistes chinensis*, the only species in the analysis without morphological castes, this was set at a value of 1. A summary of all parameter estimates for the 10 species is given in Figure S1.

Quantifying policing effectiveness. The effectiveness of policing P was quantified as $P=1-W_S$, where W_S is the relative survival of worker-laid eggs to queen-laid eggs. That is, the relative chance that worker-laid eggs are reared compared to queen-laid eggs[15-16]. Policing reduces the survival of worker-laid eggs, making P approach 100% if policing is perfectly effective. Both the queen or the workers or both can carry out policing activities, depending on species (Table S1).

W_S was estimated in one of two ways: (1) from policing trials, which compare the survival of worker-laid and queen-laid eggs (Method 1, Table S2) or (2) from the difference in the percentage of males that are workers' sons in the egg stage versus in the adult or pupal stages (Method 2, Table S3).

In Method (1), if w and q are the percentage of worker-laid and queen-laid eggs that survive until the end of a trial, then $W_S=w/q$. The survival of worker-laid and queen-laid eggs is typically measured over a period of approx. 1 day. Although the period until hatching is longer than this (3 days for honeybees[8] and 5 days for wasps[20]), this is not a problem since most of the policing generally occurs within the first hours or day after an egg is laid[6,8,21-22]. In addition, in the honeybee, the estimates of P obtained using assays that measured egg survival over 1 and 3 days are virtually identical: 98.5% and 97.7%, respectively (Table S2). Once hatched, there is no discrimination between queen and worker offspring[23].

In Method (2), the rationale is that policing should reduce the percentage of males that are workers' sons among adults compared to in the egg stage. Following this logic, W_S can be estimated as $W_S=(a/e)(1-e)/(1-a)$ where a and e are the percentage of males that are workers' sons in the adult and egg stages. The percentage of adult males that are workers' sons a was estimated from genetic studies as $a=N_W/N_A$ where N_W are the number of detected workers' sons and N_A are the number of assignable males, that is the total number of males analysed weighted by the power of detecting workers' sons[3] (Table S3). Genetic studies employed either microsatellite markers[3,4,7] or, for the honeybee, a recessive phenotypic marker[24]. The percentage of male eggs that are workers' sons e was estimated from behavioural observations of queen and worker egg-laying. If n_W and n_Q are the number of eggs laid by the workers and by the queen during a given observation period, and if a proportion m of the queen's eggs are male, then an estimated $n_M=n_W+n_Q.m$ of the eggs laid would have been male, giving $e=n_W/n_M$.

Data on the proportion of the queen's eggs that are male were obtained from sex ratio studies, correcting for the percentage of males that are workers' sons in each species (Table S3). In Vespinae wasps, workers can lay eggs into either large-celled sexual comb or combs of reused small cells used previously to rear workers. Sex ratio data were made to match behavioural observations, in coming from either large-celled sexual comb or large- and small-celled comb combined (Table S3).

For 4 out of 10 species, policing effectiveness could be estimated using both methods (Table S1). In these cases, the average was used in the statistical analysis. This was appropriate given that there was excellent agreement between the alternative estimates (Tables S2-S3). In addition, conclusions remained the same whichever of the alternative estimates were used.

Statistical analysis. Data were analysed using both raw correlations, in which each species was a data point, and phylogenetically independent contrasts (PICs)[25]. PICs are calculated from the difference in the response and predictor

phylogeny	species	% of egg-laying workers in queenright colonies	% of egg-laying workers in queenless colonies	relatedness among workers	effectiveness of policing (%) method 1	effectiveness of policing (%) method 2	effectiveness of policing (%) avg.	type of policing	queen-worker dimorphism
	Apis mellifera	0.07%	36.4%	0.30	98.5%	98.4%	**98.4%**	W	1.38
	Polistes chinensis	32.0%	26.0%	0.75		41.4%	**41.4%**	Q+W	1.00
	Vespa crabro	2.8%	11.6%	0.68	98.0%		**98.0%**	W	1.17
	Dolichovespula media	5.7%	11.3%	0.71		92.6%	**92.6%**	Q	1.33
	Dolichovespula saxonica	11.9%	12.1%	0.62		87.5%	**87.5%**	Q+W	1.32
	Dolichovespula sylvestris	9.3%	14.3%	0.68	90.3%	94.1%	**92.2%**	Q+W	1.37
	Dolichovespula norwegica	8.0%	7.9%	0.71		94.1%	**94.1%**	Q+W	1.58
	Vespula vulgaris	1.0%	29.7%	0.51	100.0%	100.0%	**100.0%**	W	1.38
	Vespula germanica	1.6%	31.7%	0.46	100.0%		**100.0%**	W	1.44
	Vespula rufa	9.2%	20.0%	0.58	67.1%	77.5%	**72.3%**	Q+W	1.50

Supplementary Figure S1. Data on the phylogeny[17], percentage of egg-laying workers (Table S1), relatedness among workers[1-7], the effectiveness of policing (Tables S2, S3) and queen-worker dimorphism in 9 species of Vespidae wasps and the honeybee *Apis mellifera*. Worker-laid eggs can be policed by the queen (Q), by workers (W) or by both (Q+W)[3,5-14,18-19].

variables across pairs of species or higher nodes that share a common ancestor[25-26] and were estimated using the *CONTRAST* module of the *Phylip* package[27]. The key predictor variables were policing effectiveness and relatedness and the response variable the (untransformed) percentage of workers with active ovaries in queenright colonies. The phylogeny was based on reference 17 (Fig. S1) and led to 9 contrasts from the 10 species. Branch lengths were set equal, corresponding to a punctuational view of evolutionary change[25], but conclusions were robust with respect to various suggested branch length transformations[25]. Statistical significance was assessed using regression through the origin[25]. In the raw data analyses, transformations to linearise relationships were applied as appropriate. The key results of the phylogenetic independent contrast analysis are shown in Fig. S2. A complementary analysis of worker egg-laying in queenless colonies as a function of relatedness is shown in Fig. S3. Queen-worker dimorphism was not significantly correlated with the percentage of egg-laying workers in either queenright (R=-0.60, p=0.07, using PICs: $F(1,8)$=4.52, p=0.07) or queenless colonies (R=-0.09, p=0.81, using PICs: $F(1,8)$=0.04, p=0.85). Hence, workers in all species were equally capable of reproducing.

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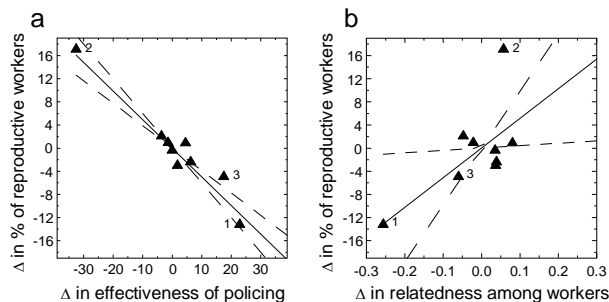
Supplementary Figure S2. Analysis of worker egg-laying in queenright colonies using phylogenetically independent contrasts (Δ). a. Contrasts in the percentage of egg-laying workers as a function of contrasts in the effectiveness of egg killing (policing). The relationship is significantly negative ($F(1,8)$=114.74, p=0.000006). **b.** Contrasts in the percentage of egg-laying workers as a function of contrasts in the relatedness among workers. The relationship is significantly positive ($F(1,8)$=6.29, p=0.04). Contrasts 1, 2 and 3 are *A. mellifera* vs. Vespidae, *P. chinensis* vs. Vespinae and (*V. vulgaris, V. germanica*) vs. *V. rufa*.
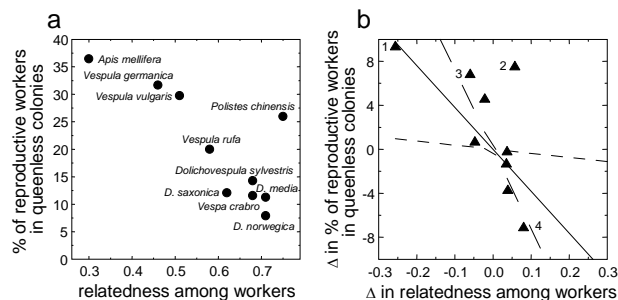
Supplementary Figure S3. The effect of relatedness on worker egg-laying in queenless colonies. a. The percentage of egg-laying workers in queenless colonies is negatively correlated with the relatedness among workers (R=-0.79, p=0.007). **b.** Contrasts in the percentage of egg-laying workers in queenless colonies as a function of contrasts in the relatedness among workers. The relationship is significantly negative ($F(1,8)$=6.53, p=0.03). Contrasts 1, 2, 3 and 4 are *A. mellifera* vs. Vespidae, *P. chinensis* vs. Vespinae, (*V. vulgaris, V. germanica*) vs. *V. rufa* and *Dolichovespula* vs. *Vespula*.

Supplementary Tables

Supplementary Table S1. Estimates of the percentage of reproductive workers in queenright and queenless colonies. The percentage of reproductive workers are the percentage that have active ovaries, i.e. with oocytes at least half the size of a freshly-laid egg. n are the number of workers dissected and C the number of colonies examined.

Species	% of reproductive workers in							
	queenright colonies	n	C	refs.	queenless colonies	n	C	refs.
Apis mellifera	0.07%	10,634	17	8	36.43%[a]	700	7	9
Dolichovespula media	5.71%	140	7	3	11.27%	275	12	11; TW, unpubl. data
Dolichovespula norwegica	7.96%	201	8	3; TW, unpubl. data	7.89%	190	10	TW, unpubl. data
Dolichovespula saxonica	11.88%	160	8	3	12.08%	149	7	TW, unpubl. data
Dolichovespula sylvestris	9.29%	140	7	3	14.29%	280	13	TW, unpubl. data
Polistes chinensis	32.00%	125	11	7	25.98%	254	16	10
Vespa crabro	2.80%	500	8	5	11.57%	216	4	TW, unpubl. data
Vespula germanica	1.59%	1,008	5	14	31.66%	259	10	11, 12, 14; TW, unpubl. data
Vespula rufa	9.17%	240	12	4	20.00%	80	4	TW, unpubl. data
Vespula vulgaris	1.04%	1,150	6	6	29.74%	269	9	13; TW, unpubl. data

[a]Measured 31 days after queen removal, when reproduction by workers peaked.

Supplementary Table S2. Estimates of the effectiveness of policing calculated from policing trials. w_{tot} and q_{tot} are the number of worker-laid and queen-laid eggs that were present or introduced at the beginning of the trials, w_{surv} and q_{surv} are the percentages of worker-laid and queen-laid eggs that survived until the end of the trials, T are the number of trials performed, C is the number of colonies used.

Species	Survival of worker-laid eggs			Survival of queen-laid eggs						Effectiveness of policing	References
	w_{surv}	w_{tot}	% of worker-laid eggs that survived ($w = w_{surv}/w_{tot}$)	q_{surv}	q_{tot}	% of queen-laid eggs that survived ($q = q_{surv}/q_{tot}$)	T	C	measured over period of	$P = 1\text{-}w/q$	
Apis mellifera	9[a]	1340	0.67%	661	1461	45.24%	24	20	24 h	98.52%	23
Apis mellifera	3[a]	161	1.86%	465	581	80.03%	15	15	3 d	97.67%	8, 28
Dolichovespula sylvestris	22	237	9.28%	213	222	95.95%	16	8	16 h	90.33%	22
Vespa crabro	1	79	1.27%	46	72	63.89%	3	6	16 h	98.02%	21
Vespula germanica	0	114	0.00%	36	114	31.58%	4	2	2 d	100.00%	14
Vespula rufa	9	28	32.14%	199	204	97.55%	12	2	24 h	67.05%	4
Vespula vulgaris	0	120	0.00%	80	120	66.67%	3	2	16 h	100.00%	6

[a]A fourth worker egg that survived was probably a queen-laid egg moved from another location in the hive as it already hatched within 1 day after first being observed, implying it could not have been laid there[8]

Supplementary Table S3. Estimates of the effectiveness of policing calculated from the difference between the percentage of males that are workers' sons as adults vs. in the egg stage. n_W and n_Q are the number of worker and queen ovipositions observed, m is the % of queen's eggs that are male, n_M is the estimated number of queen ovipositions that were male, N_W is the number of detected adult males that are workers' sons, N_A is the number of assignable males (the total number of males assayed, weighted by the power to detected workers' sons[3]) and C are the number of colonies that were examined for egg or adult male parentage.

Species	Parentage of eggs						Parentage of adult males				Effectiveness of policing	References
	n_W	n_Q	% of queen's eggs that are male (m)	$n_M = n_W + m.n_Q$	% of male eggs that are workers' sons ($e = n_W/n_M$)	C	N_W	N_A	% of adult males that are workers' sons ($a = N_W/N_A$)	C	$P = 1\text{-}((a/e) \times (1\text{-}e)/(1\text{-}a))$	
Apis mellifera	-	-	-	-	7.30%[a]	4	37	28,980	0.13%	11	98.38%	24, 29
Dolichovespula media	12	23	47.77%[b]	22.99	52.20%[c]	3	11	148	7.43%[c]	8	92.65%	3
Dolichovespula norwegica	19	84	49.25%[d]	60.37	31.15%[e]	5	4	152	2.63%[c]	8	94.12%	3; TW, unpubl. data
Dolichovespula saxonica	164	91	42.58%[f]	202.74	80.89%[c]	4	52	150	34.67%[c]	9	87.46%	3, 30, 31
Dolichovespula sylvestris	361	520	37.56%	556.31	64.89%[e]	8	15	154	9.77%[c]	10	94.14%	3, 22, 32
Polistes chinensis	89	90	55.56%	139.00	64.03%	5	228	426	51.07%[g]	22	41.36%	7, 33
Vespula rufa	28	202	24.83%	78.16	35.83%[e]	2	33	296	11.15%[e]	13	77.52%	4
Vespula vulgaris	4	29	50.60%	18.67	21.42%	1	0	171	0.00%	9	100.00%	6, 13
Vespula vulgaris	-	-	50.60%	-	28.60%[h]	6	0	171	0.00%	9	100.00%	6, 13

[a]A complex procedure was used to calculate e[29]; [b]Colonies produce 49.70% males[34], 7.43% of which are workers' sons[3], giving m=47.77%; [c]Based on data from large and small-celled comb; [d]Sexual comb contains 49.92% males[35], 2.63% of which are workers' sons[3], giving m=49.25%; [e]Based on data from large-celled sexual comb; [f]Colonies produce 53.16% males[34,36,37], 34.67% of which are workers' sons[3], giving m=42.58%; [g]The published value of 39.1% was corrected for the mean power to detect workers' sons, 79.3% (K. Tsuchida, pers. comm.), giving a=51.07%; [h]e was estimated from rates of worker ovary activation and the fecundity of workers measured in queenless colonies[13]