

between trait values and age for males and females, and used maximum values of the curves for each sex. In particular, when relationships were decreasing linear or concave quadratic, we used mean values at 2 years of age; for convex quadratic relationships we used maximum values for male and female curves, and for asymptotic relationships we used the asymptotes.

Dimorphisms of linear measurements were standardized by elevating them to the third power and surfaces were multiplied by their square root, to make them comparable with volumes and weights. Dependent variables were explored for normality and homogeneity of variances. Crown height was transformed to  $\ln(\text{crown height} + 1)$  to obtain linear relationships with age. The significance level was set at  $P = 0.05$  and all  $P$  values are two-tailed.

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## A socially enforced signal of quality in a paper wasp

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Organisms use signals of quality to communicate information about aspects of their relative phenotypic and genetic constitution<sup>1–4</sup>. Badges of status<sup>5–7</sup> are a subset of signals of quality that reveal information about an individual's size and dominance. In general, signals of quality require high and differential costs to remain honest<sup>1,2</sup> (that is, prevent low-quality cheaters from exploiting any fitness benefits associated with communicating high quality). The theoretically required costs for badges of status remain controversial because the development (or 'production') of such signals often seems to be relatively cost-free<sup>5,6,8</sup>. One important hypothesis is that such signals impose social (or 'maintenance') costs incurred through repeated agonistic interactions with other individuals<sup>9–12</sup>. However, convincing empirical evidence for social costs remains elusive<sup>6,7</sup>. Here we report social costs in a previously undescribed badge of status: the highly variable black facial patterns of female paper wasps, *Polistes dominulus*. Facial patterns strongly predict body size and social dominance. Moreover, in staged contests between pairs of unfamiliar wasps, subordinate wasps with experimentally altered facial features ('cheaters') received considerably more aggression from the dominant than did sham controls, indicating that facial patterns are signals and that dishonest signalling imposes social costs.

Variation in the number, size and shape of black spots on the clypeus of *P. dominulus* (Box 1) is remarkable (Fig. 1). Given the signalling potential<sup>13</sup> of these facial patterns, we tested whether they are related to quality by evaluating their relationship to body size (an important predictor of dominance<sup>14,15</sup>) and social dominance as determined by pair-wise contests between unfamiliar wasps.

Clypeus spots are strongly correlated with overall body size. Multiple regression yielded both spot number and percentage of clypeus pigmented black as significant predictors of head width (Fig. 2, total regression:  $N = 158$ ,  $F = 5.86$ ,  $r^2 = 0.070$ ,  $P = 0.0035$ ; spot number:  $t = 2.07$ ,  $P = 0.040$ ; percentage of clypeus black:  $t = 2.01$ ,  $P = 0.046$ ). In *Polistes*, head width is the measure of body size most highly correlated with other body size measurements<sup>16</sup>.

Facial patterns also predict social dominance beyond their relationship with body size. To control for the effects of body size on dominance, we paired similarly sized unfamiliar foundresses and observed their behaviour as they battled for dominance (similarity in mass between pairs:  $r^2 = 0.83$ ). The alpha (dominant) wasp was easily identified by 'mount' displays, where the beta wasp lowers her antennae and allows the alpha to climb on her head<sup>14</sup>. Differences in spot number between contestants significantly predicted dominance, with more dominant wasps having more spots (Table 1). Percentage of clypeus black was not a significant predictor of dominance in the trials, however wasps with relatively less black pigment tended to have higher dominance (Table 1).

We explored the signal value of clypeus patterns in more detail by conducting a pattern analysis on the wasps used in the dominance trials. We quantified the amount and position of black pigment on

each wasp by converting the area of the clypeus containing the population-wide badge variability into a rectangular 30 × 60-pixel bitmap. We then used the bitmap to determine the amount of black pigment present in each of the 60 vertical strips along the horizontal gradient of the clypeus (Fig. 3a). In the overall population, the pigment and pigment variability was concentrated between two prominent peaks of pigment, located on either side of the centre of the clypeus (Fig. 3b). These peaks were much more pronounced in alpha wasps than beta wasps (Fig. 3c), suggesting that more

dominant wasps tend to have more 'broken' facial patterns.

To quantify the difference between alphas and betas, we calculated a 'badge brokenness index' for each wasp as the variability (standard deviation) of amount black pigment deposited along the horizontal gradient located between the two peaks. Overall, mean badge brokenness was significantly higher in alphas than in betas (Fig. 3d,  $t_{120} = 3.35$ ,  $P = 0.0011$ ). Furthermore, badge brokenness was the only significant predictor of dominance when included with spot number and percentage of clypeus black in a multiple logistic regression (as computed in Table 1: whole model,  $r^2 = 0.105$ , chi-square = 8.86, d.f. = 1,  $P = 0.003$ ; Brokenness, Wald chi-square = 7.52,  $P = 0.006$ ). The high dominance (Table 1) and high brokenness index (Fig. 3d) of  $\geq 2$ -spot wasps contributed strongly to this relationship, but brokenness also predicted dominance in contests between pairs of 1-spot wasps ( $N = 16$  trials, Wald chi-square = 4.79,  $P_{(1\text{-tailed})} = 0.044$ ). This suggests brokenness is a more general predictor of dominance than spot number *per se*. Badge brokenness is also correlated with body size: in the random sample of wasps collected for morphological analysis (see Fig. 2), brokenness was significantly correlated with head width ( $N = 158$ ,  $r^2 = 0.028$ ,  $F = 4.53$ ,  $P = 0.035$ ). The brokenness index is a particularly useful parameter because it collapses a wasp badge's degree of advertised dominance into a singular variable.

Clypeus patterns in *P. dominulus* share four similarities with typical melanin-based badges of status in birds (Box 1). They are: (1) variable, (2) visible<sup>13</sup> (located on the part of the body most apparent during face-to-face aggressive encounters), (3) associated with body size and (4) associated with dominance. What keeps the relationship between facial patterns and dominance 'honest'? Clypeus spots (most likely eumelanin<sup>17</sup>) seem to have low differential production costs because the spots account for less than 1% of the total black pigmentation of *P. dominulus* and the rest of the pigment seems identical from wasp to wasp.

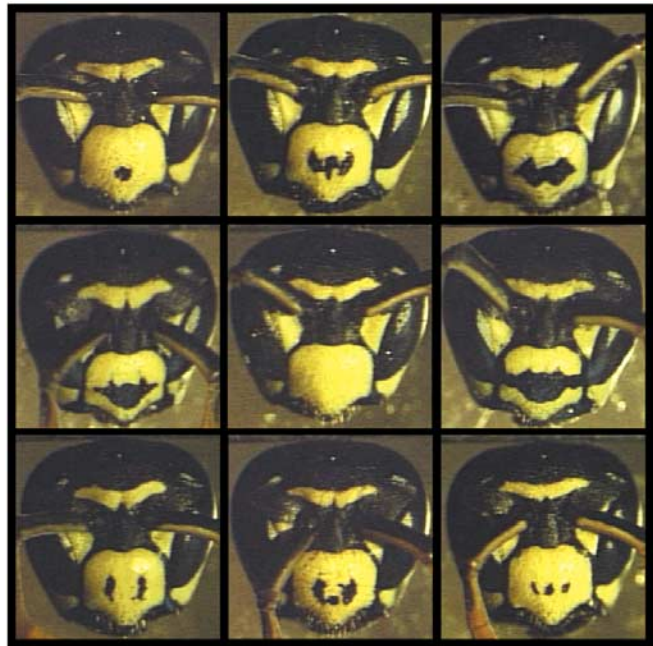
Box 1

**Badges of status, social costs and wasps**

**Badges of status** The classic examples are signals used to settle minor dominance contests in flocks of birds<sup>5</sup>. For example, the size of melanin-based throat patches in a variety of species reflects aggression during feeding<sup>6,24</sup>. However, badges of status are also used in other contexts. Territorial defence is related to the size of the white forehead patch in collared flycatchers *Ficedula albicollis*<sup>25</sup> and the redness of the carotenoid-based epaulets in red-shouldered widowbirds *Euplectes axillaris*<sup>26</sup>. Badges of status appear to be honest (that is, reliable predictors of dominance), but it is unclear how the honesty of these signals is maintained<sup>6,8</sup>. Indeed they are often argued to have low production costs<sup>5,8</sup>: for example, the pigment-less badge of the collared flycatcher is probably based on the *cheapest* form of feather development. Without some type of cost, these signalling systems would be vulnerable to the evolutionary spread of a 'cheater' strategy: subordinate individuals which develop, not necessarily with intent, badges associated with higher dominance.

**Social costs** One hypothesis is that honesty can be maintained if cheaters suffer social costs that outweigh any benefits of cheating<sup>5-7,9-12</sup>. The main line of support for social costs comes from studies demonstrating that individuals with experimentally altered badges receive more aggression than honest individuals<sup>6,7,9</sup>. However, many studies have failed to find evidence for increased aggression towards experimentally created cheaters (see ref. 6 for review), and the positive support is rife with problems stemming from difficult to interpret experiments (see refs 6, 27) and potential confounds such as the signalling of individual identity<sup>4,13,24,28,29</sup>, age-group<sup>24,29,30</sup> or gender<sup>24,29,30</sup> rather than status *per se*. In this study we address these problems by evaluating behaviour in both participants of pair-wise dominance trials between unfamiliar contestants of the same age and sex. Social costs are the major hypothesis to explain the honesty of badges of status in birds<sup>6</sup> and many other taxa<sup>7</sup>, although they have yet to be demonstrated conclusively<sup>6,7</sup>.

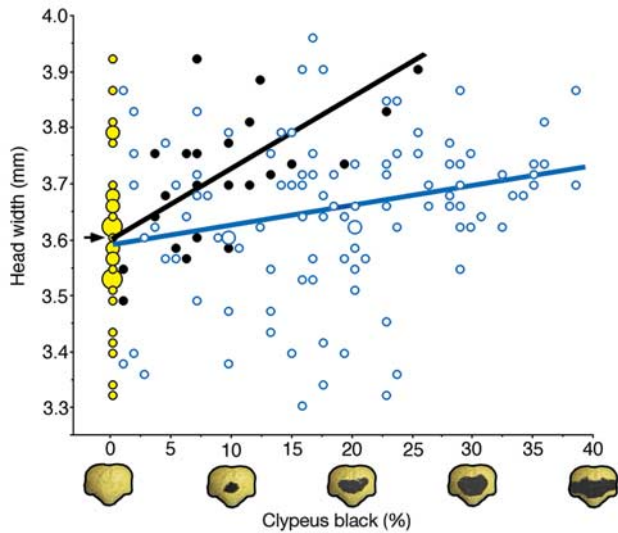
***Polistes dominulus*** Dominance is a key feature in the lives of these common eusocial insects<sup>14</sup>. After overwintering, newly emerged queens found new colonies, often co-operatively with other co-foundresses<sup>15</sup>. Foundresses fight vigorously to establish dominance rank because dominance determines the amount of reproduction each foundress secures<sup>14</sup>. Dominance probably has an important role in settling conflict in many other contexts including the order of queen succession, division of labour, sharing of food and the probability of becoming a future queen. Among insects, these paper wasps are good candidates to evolve visually based badges of status because they are visually acute, diurnal, open living and highly social.



**Figure 1** Portraits of nine *P. dominulus* foundresses collected in Ithaca, New York, representing some of the diversity in facial patterns. The central wasp has no black clypeus pigmentation, the remaining top 5 wasps have 1 black spot each, and the bottom 3 wasps have 2, 2 and 3 spots, respectively. In 158 randomly collected foundresses, 19.6% of foundresses had an entirely yellow clypeus, 65.8% had a single black spot, 12.7% had two spots and 1.9% had three spots. On average 13% ( $\pm 11$  s.d.) of a wasp's clypeus was pigmented black, and this value ranged broadly from 0 to 39%.





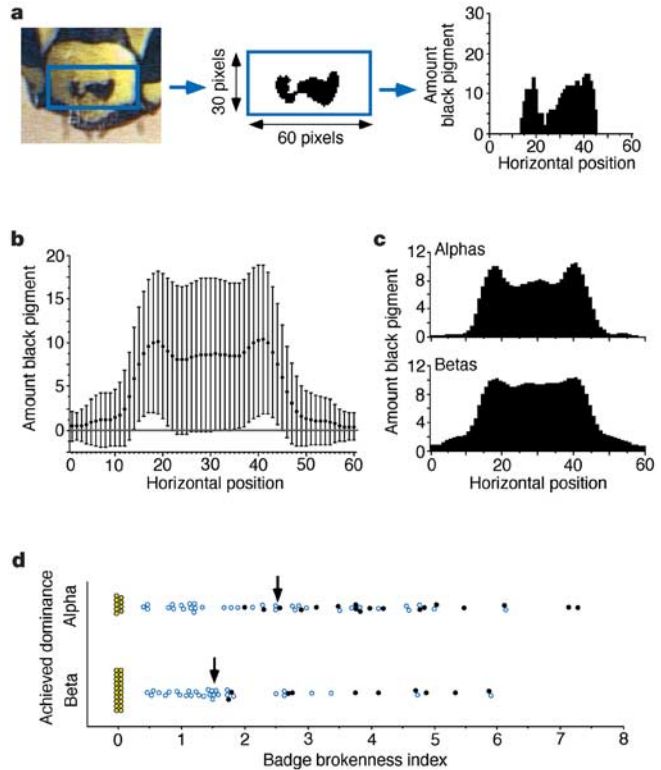


**Figure 2** Head width versus clypeus variability. 158 foundresses were collected from 40 single-foundress and 49 multiple-foundress colonies across Tompkins County, New York (May 2001). Model 1 regression in wasps with  $\geq 2$ -spots,  $y = 1.096x + 3.605$ ,  $N = 23$ ,  $r^2 = 0.36$ ,  $F = 12.14$ ,  $P = 0.002$  (black line and black filled circles). Wasps with 1 spot,  $y = 0.302x + 3.590$ ,  $N = 104$ ,  $r^2 = 0.046$ ,  $F = 4.94$ ,  $P = 0.029$  (blue line and blue open circles). Mean (= 3.604 mm) (arrow) and distribution (yellow circles), in wasps with no spots. The slope of the  $\geq 2$ -spot regression line is  $3.6 \times$  steeper than the 1-spot line, however this difference is not statistically significant (Student's  $t$ -test for slopes,  $t = 1.75$ ,  $P = 0.08$ ). Increasing point sizes correspond with one, two and three overlapping data points, respectively.

We tested whether black spots had social costs (that is, costs associated with signal maintenance and accrued during repeated agonistic interactions (Box 1)). We evaluated two critical tests of the hypothesis. Firstly, do alphas react to natural 'cheaters', that is, subordinate wasps who possess badges associated with higher brokenness indices? We specifically predicted that subordinates with higher brokenness indices should receive more aggression from dominants than subordinates with lower brokenness indices. Secondly, do wasps react to experimentally created 'cheaters'<sup>9,13</sup>? We specifically predicted that wasps whose badges are altered so they no longer reflect their bearers' true behavioural dominance should receive more aggression from opponents than wasps whose badge appearances were not changed.

To test responses to natural cheaters, we scored aggression between contestants after dominance was established (after one wasp submitted to a mount attempt by the other). Alphas reinforced their dominance through repeated mounts of betas. As predicted, the post-dominance mount rate of alphas was strongly and positively correlated with the badge brokenness of betas (Fig. 4). Therefore, after dominance has been determined, subordinate wasps pay higher social costs if they have badges associated with higher dominance.

To test responses to experimentally created cheaters, we conducted a second set of dominance trials (as above). In these trials, the badge of one wasp from each pair was experimentally manipulated<sup>13</sup> into one of three treatment groups: (1) sham controls were



**Figure 3** Relationship between pigment deposition and dominance in unmanipulated wasps (paired by mass). **a**, Example of pattern analysis, the badge of each wasp was converted into a  $30 \times 60$  pixel bitmap to quantify the position and amount of black pigment. **b**, Mean amount of pigment ( $\pm$ s.d.) along the horizontal gradient of the badge bitmaps for wasps used in the dominance trials ( $N = 122$ ). **c**, Mean pigment amounts for alphas ( $N = 61$ ) and betas ( $N = 61$ ). **d**, Achieved dominance as a function of badge 'brokenness', a measure of variability in black pigment along the central third of the clypeus ( $N = 122$ ). Arrows denote means. The colour of each point corresponds with spot number: yellow = no spot, blue = 1-spot and black =  $\geq 2$ -spots.

painted on the clypeus without altering their visual appearance, (2) negative and (3) positive 'cheaters' were painted on the clypeus to reduce, or increase, respectively, their apparent badge rank. The other wasp in each pair was not manipulated (hereafter, 'unpainted').

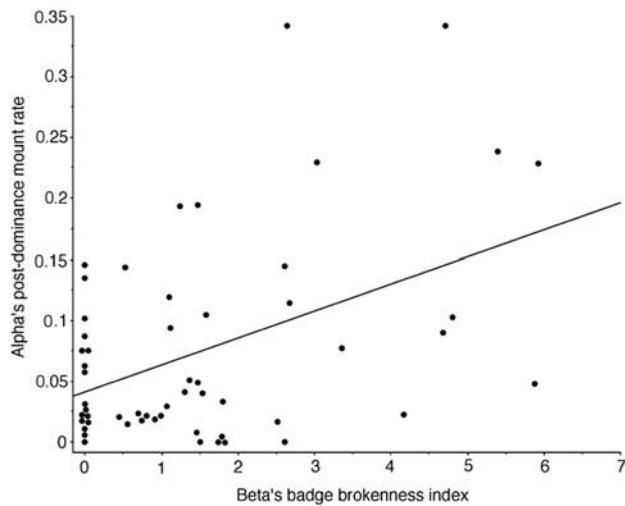
The manipulation had little impact on behaviour before dominance establishment. Painting did not influence achieved dominance rank (in 29 of 72 trials the manipulated wasp achieved alpha position, chi-square = 2.72, d.f. = 1,  $P = 0.10$ ), and there was no effect of treatment group on probability of becoming dominant (chi-square = 0.41, d.f. = 2,  $P > 0.50$ ). Thus, positive cheaters were no more likely to be alpha than controls or negative cheaters. Threat rates (Fig. 5a) and mount-attempt rates (Fig. 5b) were similar in manipulated and unpainted wasps and did not depend on treatment.

Post-dominance behaviour was affected strongly by the badge alterations. Beta cheaters received significantly more post-dominance mounts from alphas than did beta sham controls (Fig. 5c). Betas manipulated to advertise high dominance received approxi-

**Table 1** Mean spot number and percentage of clypeus pigmented black in winners versus losers of dominance contestants (paired by mass).

	Mean ( $\pm$ s.e.) of winners	Mean ( $\pm$ s.e.) of losers	Wald chi-square*	P
Spot number	1.230 $\pm$ 0.013	0.853 $\pm$ 0.012	7.90	0.010
Percentage of clypeus black	10.4 $\pm$ 0.2	13.4 $\pm$ 0.2	3.28	0.070

\*logistical multiple regression of the signed pair-wise differences of these variables as predictors of dominance. The dependent variable was whether a single focal wasp of each pair (assigned randomly) was winner (1) or loser (0). The interaction term between independents was not significant so we removed it from the model. The final regression was significant:  $N = 61$  trials,  $r^2 = 0.119$ , likelihood ratio test chi-square = 10.07, d.f. = 3,  $P = 0.007$ . When differences in percentage of clypeus black were also removed from the model in step-wise fashion, differences in spot number remained a significant predictor of dominance (Wald chi-square = 5.59,  $P = 0.018$ ).



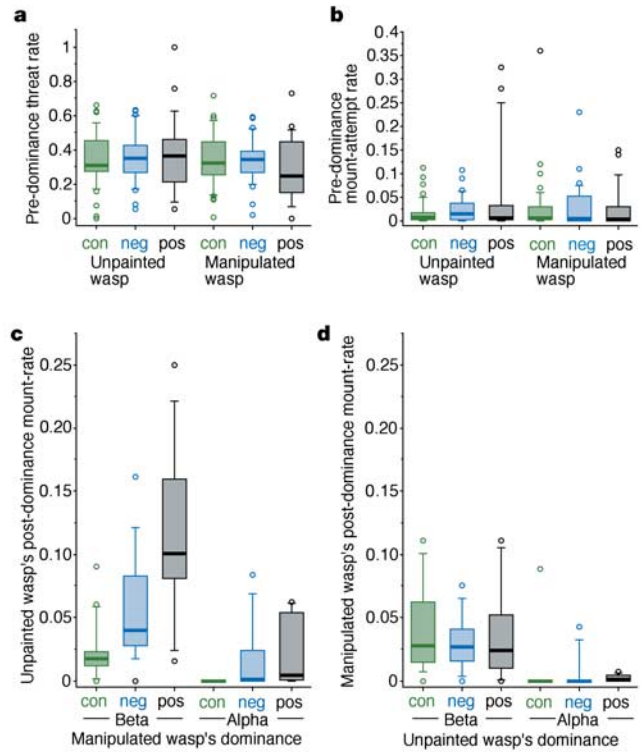
**Figure 4** Relationship between post-dominance mount rate by alpha versus beta's badge brokenness. Rates were recorded in unmanipulated wasp contestants (paired by mass) and are reported as  $\log(\text{events}/\text{min} + 1)$ . Model 1 regression:  $y = 0.221x + 0.041$ ,  $N = 55$  trials,  $r^2 = 0.18$ ,  $F = 12.97$ ,  $P = 0.0007$ .

mately six times more aggression than beta sham controls, and roughly twice the aggression of wasps painted to advertise low dominance. In strong contrast, manipulated wasps who became alpha were similarly aggressive to the unpainted beta independent of their treatment group (Fig. 5d). Furthermore, their aggression levels were similar to those expressed by unpainted alphas towards beta sham controls (analysis of variance (ANOVA),  $F_{3,42} = 0.97$ ,  $P = 0.42$ ). Thus badge alteration did not influence how manipulated individuals treated their opponents, but it did influence strongly how they were treated by these opponents. Interestingly, unpainted betas challenged cheating alphas more frequently than sham control alphas (Fig. 5c). Finally, dominance 'switches' (where the beta successfully claimed alpha position after initial dominance was established) were only observed ( $N = 10$ ) in cheater treatments (Fisher exact  $P = 0.002$ ). Thus facial pattern alteration interfered with accurate exchange of dominance information between contestants, indicating that the facial patterns are a signal.

These results suggest that dishonest status advertisement in *P. dominulus* is kept in check through social costs. Wasps whose badges dishonestly signal their bearers' quality receive more aggression. Increased aggression is costly<sup>18</sup> because it imposes physiological and time costs (for example, see ref. 19), and presumably increases the risk of injury, thereby reducing group productivity (for example, see ref. 20). Because our experimental design allows us to exclude confounding hypotheses (see Box 1), these results represent the most convincing evidence for social costs to date. Although subordinates with increased badge quality received the most aggression, subordinates with reduced badge quality also received more aggression than sham control subordinates. In both cases, the increased aggression probably results from the alpha's detection of a greater incongruence<sup>9</sup> between badge phenotype and other quality cues (for example, behavioural and/or pheromonal<sup>21</sup>) in the cheater subordinates.

The visual signal of status is probably important in many contexts, as dominance is such a critical aspect of the social behaviour of *P. dominulus*<sup>14</sup>. Social costs seem strongest after dominance establishment, so fitness benefits associated with honest signals are probably felt then too: through the signals' effects on conflict settlement regarding dominance succession, relative reproduction, sharing of resources and division of labour.

Wasps with multiple spots (or more generally, more broken patterns) are more dominant, suggesting that these phenotypes



**Figure 5** Dominance behaviour in trials where one wasp's facial appearance was experimentally manipulated. Con, sham control; neg, negative cheaters; pos, positive cheaters. Rates are reported and analysed as  $\log(\text{events}/\text{min} + 1)$ . Box plots show medians, 10th, 25th, 75th and 90th percentiles and outlying data points. **a, b**, Threat rates (**a**) and mount-attempt rates (**b**) were similar in unpainted and manipulated wasps before dominance establishment (ANOVA: threat rates,  $F_{5,186} = 0.61$ ,  $P = 0.70$ ; mount-attempt rates,  $F_{5,186} = 1.21$ ,  $P = 0.30$ ). **c**, Post-dominance mount rates by unpainted wasps towards manipulated wasps. Analysed with two-factor ANOVA using treatment and unpainted wasp's dominance (alpha or beta) as independent variables. Mount rate varied significantly between treatments ( $F_{2,65} = 11.12$ ,  $P < 0.0001$ ). **d**, Post-dominance mount rates by manipulated wasps towards unpainted wasps were similar among treatments ( $F_{2,65} = 0.34$ ,  $P = 0.72$ ).

are more costly. This observation is not consistent with high production costs of pigmentation because wasps with one spot (which tend to be less dominant) have about twice as much black pigment as wasps with  $\geq 2$  spots (mean percentage of clypeus black in one-spots = 18.4%, in  $\geq 2$  spots = 9.6%,  $t_{125} = 4.09$ ,  $P < 0.0001$ ). However, this observation is consistent with social costs. An important difference between social costs and production costs is that social costs depend directly on variance in how the signal is perceived (that is, its obviousness) rather than on variance in the absolute state of the signal (for example, its size). Researchers have long known that the hymenopteran compound-eye/visual system is particularly attuned to the amount of disruption in a pattern<sup>22</sup>. Therefore, the most 'broken' facial patterns may be the most visually apparent phenotypes to receivers. Wasps with more broken patterns may be broadcasting a more obvious signal, and hence have a phenotype associated with higher social costs. □

**Methods**

**Morphology**

We mounted the head of each wasp against a ruler affixed to the viewing tray of a  $\times 40$ -dissecting microscope. The faces were videotaped with a digital video camera mounted onto the microscope using a Sony CCD camera. We analysed frames from these videos imported into Adobe Photoshop (see ref. 8) to determine (1) the percentage of the clypeus that was pigmented black ( $R_1 = 0.99$ ,  $F_{10,11} = 676$ ,  $P < 0.0001$ ), (2) the number of spots and (3) the maximum width (in mm) of the head capsule ( $R_1 = 0.99$ ,  $F_{10,11} = 236$ ,  $P < 0.0001$ ) (repeatabilities ( $R_i$ ) calculated using different images of the same wasps).

## Size analysis

Because multiple foundresses are often sisters<sup>23</sup>, the size analysis (Fig. 2) is not completely independent of genetic relatedness. However, there were no differences between wasps from single and multiple foundress colonies in head width ( $t_{156} = -0.66$ ,  $P = 0.51$ ), spot number ( $t_{156} = -0.51$ ,  $P = 0.61$ ) or percentage of clypeus black ( $t_{156} = -1.57$ ,  $P = 0.12$ ). Furthermore, when mean colony values were used in multiple regression, spot number (but not percentage of clypeus black) was still a significant predictor of head width (total regression:  $N = 89$  colonies,  $r^2 = 0.09$ ,  $F = 4.29$ ,  $P = 0.017$ ; spot number:  $t = 2.08$ ,  $P = 0.040$ ; percentage of clypeus black:  $t = 1.16$ ,  $P = 0.25$ ).

## Dominance trials

144 recently emerged foundresses were collected in Ithaca, New York (April–May 2002), weighed, marked for individual identification with enamel paint on the thorax and isolated in a small holding container for 0.5–6 h until their trial began. For each trial ( $N = 72$ ), two wasps collected from sites >5 km apart were matched for weight, placed in a  $7.5 \times 12.5 \times 4$  cm plastic arena, and their interactions were videotaped for 2 h. After the trial, the contestants' faces were photographed and scored with Photoshop. Videos were scored for two parameters: (1) Dominance: foundresses battled for dominance using the natural range of dominance interactions. *Polistes* wasps aggressively oppose attempted mounts by subordinate wasps, but lower their antennae and remain still to allow mounting by dominants<sup>14</sup>. Dominance was considered established when one wasp (= beta) lowered her antennae and allowed the other wasp (= alpha) to mount her. 11 trials where the apparent subordinate never submitted were excluded from further analyses. (2) Post-dominance aggression: to test our first prediction, we recorded the number of mounts subordinates received after dominance was established. Because the interval of post-dominance behaviour varied between trials depending on when dominance was established ( $N = 55$ ,  $x = 59.6$  min  $\pm$  31.6 s.d., range = 5.0 to 121.5), our measure of post-dominance mount rates could be affected if mount rates change with time. However mount rate was not related to post-dominance observation time ( $r^2 = 0.00$ ,  $F = 0.029$ ,  $P = 0.87$ ). Six trials where alpha's identity was determined, but we did not obtain videos, were excluded from the analyses of post-dominance behaviour.

## Manipulation experiments

192 recently emerged foundresses were collected in Ithaca, New York (April–May, 2003). Pairs of wasps (collected from sites >5 km apart and similar in mass ( $r^2$  between pairs = 0.92)) comprised an unpainted (unmanipulated), and a painted (manipulated)<sup>13</sup> individual. Each unpainted wasp had a single clypeus spot (indicating average dominance) and received a silver dot on her back for identification. Painted wasps had a range of facial patterns, from 0 to 3 spots, and were placed into one of three treatment groups: (1) 'sham controls' ( $N = 44$ ) were painted without altering their facial appearance using yellow and/or black Testors enamel paint (no.1114 and no.1147, respectively); (2) 'positive cheaters' ( $N = 23$ ) had their original 0 or 1 spot markings altered with black and/or yellow paint to 2 spots; and (3) 'negative cheaters' ( $N = 29$ ) had their original 1 or 2 spot markings altered with yellow paint to 0 spots. The paint was allowed to dry for 20 min before the two wasps were placed in an arena and videotaped for 2 h (as above). Tapes were later analysed for dominance behaviour by E.A.T., blind to treatment group. In each trial, we recorded: (1) dominance (as above; 24 trials where there was no submission by the apparent subordinate were excluded from analyses requiring alpha's identity); (2) pre-dominance threat rate (threat = the initiator lunges towards the recipient) and mount-attempt rate by each wasp; and (3) post-dominance mount rate by each wasp. Post-dominance observation time ( $N = 71$ ,  $x = 92.3$  min  $\pm$  27.2 s.d., range = 17.9 to 120.8) was not related to mount rate in all treatments pooled ( $r^2 = 0.00$ ,  $F = 0.001$ ,  $P = 0.97$ ) or in treatments analysed separately (all  $P > 0.17$ ). One trial where there was only one minute of post-dominance behaviour was excluded from the mount rate analysis. In 10 trials (5 in each cheater treatment), the beta successfully assumed the dominant position as indicated by successfully mounting the alpha (that is, alpha submitted).

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## Environmental biosafety and transgenic potato in a centre of diversity for this crop

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The Nuffield Council on Bioethics<sup>1,2</sup> suggests that introgression of genetic material into related species in centres of crop biodiversity is an insufficient justification to bar the use of genetically modified crops in the developing world. They consider that a precautionary approach to forgo the possible benefits invokes the fallacy of thinking that doing nothing is itself without risk to the poor. Here we report findings relevant to this and other aspects of environmental biosafety for genetically modified