THE ROYAL SOCIETY

*doi* 10.1098/rspb.2001.1754

# Helping effort and future fitness in cooperative animal societies

**Michael A. Cant*** **and Jeremy Field**

*Department of Biology, University College London, Wolfson House, 4 Stephenson Way, London NW1 2HE, UK*

Little attention has been paid to a conspicuous and universal feature of animal societies: the variation between individuals in helping effort. Here, we develop a multiplayer kin-selection model that assumes that subordinates face a trade-off because current investment in help reduces their own future reproductive success. The model makes two predictions: (i) subordinates will work less hard the closer they are to inheriting breeding status; and (ii) for a given dominance rank, subordinates will work less hard in larger groups. The second prediction reflects the larger pay-off from inheriting a larger group. Both predictions were tested through a field experiment on the paper wasp *Polistes dominulus*. First, we measured an index of helping effort among subordinates, then we removed successive dominants to reveal the inheritance ranks of the subordinates: their positions in the queue to inherit dominance. We found that both inheritance rank and group size had significant effects on helping effort, in the manner predicted by our model. The close match between our theoretical and empirical results suggests that individuals adjust their helping effort according to their expected future reproductive success. This relationship has probably remained hidden in previous studies that have focused on variation in genetic relatedness.

**Keywords:** helping behaviour; cooperative breeding; eusociality; inheritance

## 1. INTRODUCTION

Cooperatively breeding animals, in which adults help rear offspring that are not their own, have long been the focus of research aimed at understanding the evolution of cooperation and altruism (Hamilton 1964). Considerable progress has been made in elucidating the ecological and genetic conditions under which natural selection will favour helping over breeding (Emlen 1991; Seger 1991). By contrast, relatively few studies have focused on the problem of why some individuals provide much more help than others (Schmid-Hempel 1990; Reeve 1992; Heinsohn & Legge 1999; Clutton-Brock *et al.* 2000). One possibility—derived from the inclusive fitness theory (Hamilton 1964)—is that variation in helping effort reflects variation in genetic relatedness among group members, as closer kin are expected to provide a greater level of help (see Emlen 1991). Although some studies have found the predicted positive correlation between helping effort and kinship, several others have not (see Clutton-Brock *et al.* (2000) and references therein). This inconsistency across studies has led some authors to suggest that variation between group members in the costs of helping, rather than in relatedness, might be the prime determinant of observed patterns of helping (Heinsohn & Legge 1999; Clutton-Brock *et al.* 2000).

The short-term costs of helping can include loss of condition or weight, or a heightened risk of injury or predation (Schmid-Hempel & Wolf 1988; Reeve 1991; O'Donnell & Jeanne 1992; Clutton-Brock *et al.* 1999, 2000). From the perspective of life-history theory, this means that helpers will face a trade-off between current investment in help and their own future reproductive success, in much the same way as solitary animals face a trade-off between current and future allocation of energy for reproduction (West-Eberhard 1981; Stearns 1992). Here, we use this concept of a current versus future trade-off to develop a kin-selection model to account for variation in helping effort. We then present the results of an experimental field study showing that our model successfully explains variation in helping effort between paper wasp co-foundresses.

## 2. THE MODEL

Consider a subordinate in a stable group who can invest in the current brood of the dominant breeder at a cost to her own potential for future reproduction. For example, helping might reduce her survivorship or condition. Let $w(h)$ denote the expected future direct fitness of the subordinate (or 'reproductive value'; see Stearns 1992), as a function of the amount of help that she provides, $h$. Let $k(h)$ denote the increase in the direct fitness of the dominant when the subordinate helps at a level $h$. The inclusive fitness pay-offs of the subordinate and of the dominant as a function of $h$ can then be written

$$W_{\mathrm{sub}}(h) = w(h) + rk(h) \qquad (2.1)$$

and

$$W_{\mathrm{dom}}(h) = k(h) + rw(h), \qquad (2.2)$$

where $r$ is the coefficient of relatedness between the dominant and the subordinate.

Next, we specify the functions $w(h)$ and $k(h)$. Because helping is assumed to be costly, $w(h)$ is a decreasing function of $h$. For simplicity, let

$$w(h) = w_0(1 - ch), \qquad (2.3)$$

where $w_0$ is the expected future direct fitness of a subordinate who stays in the group but provides no help, and

---

*Author and address for correspondence: Department of Neurobiology and Behavior, Seeley G. Mudd Hall, Cornell University, Ithaca, NY 14853, USA (mc282@cornell.edu).

*Received* 25 January 2001 *Accepted* 22 May 2001

$c$ measures the cost of helping. The maximum level of help permitted is $1/c$, for which $w(h) = 0$.

Increasing individual investment in the current brood is assumed to bring diminishing benefits in terms of productivity, so that $k(h)$ is a positive, decelerating function of $h$. Again for simplicity, we use

$$k(h) = b(1 - \mathrm{e}^{-qh}), \tag{2.4}$$

where $b$ is the asymptotic value of the benefit conferred by the subordinate and the parameter $q$ determines how rapidly the marginal benefits of help diminish. Qualitatively similar results are obtained from a range of other functions, for which the productivity benefits of helping, $k(h)$, minus the fitness costs involved, $(w_0 - w(h))$, are maximized at some intermediate level of help.

The optimum level of help for the subordinate to provide is found by substituting our chosen expressions for $w(h)$ and $k(h)$ into equation (2.1) and maximizing with respect to $h$. The solution is given by

$$\hat{h}_{\mathrm{sub}} = \frac{1}{q}\ln\left(\frac{bqr}{cw_0}\right). \tag{2.5}$$

Similarly, maximizing equation (2.2) with respect to $h$ gives the optimum level of help for the subordinate to provide from the perspective of the dominant. The solution is

$$\hat{h}_{\mathrm{dom}} = \frac{1}{q}\ln\left(\frac{bq}{rcw_0}\right). \tag{2.6}$$

These two expressions set lower and upper limits, respectively, on the level of subordinate help according to which individual controls the rate at which the subordinate works. When the subordinate is completely free to choose her own level of help, she should work at rate $\hat{h}_{\mathrm{sub}}$. At the opposite extreme, when the dominant exercises full control over helping behaviour (e.g. through the use or threat of aggression), the subordinate will be forced to work at rate $\hat{h}_{\mathrm{dom}}$. When each player exercises partial control, the subordinate will work at some level intermediate between $\hat{h}_{\mathrm{sub}}$ and $\hat{h}_{\mathrm{dom}}$.

A central result of this simple model, apparent from expressions (2.5) and (2.6), is that an increase in the future fitness of the subordinate, $w_0$, leads to a decrease in both $\hat{h}_{\mathrm{sub}}$ and $\hat{h}_{\mathrm{dom}}$. That is, regardless of whether the dominant or the subordinate herself controls helping behaviour, a subordinate with high expected future fitness should work less hard for the dominant than one with little or no expectation of direct fitness in the future.

To test whether subordinates adjust their level of help according to their expected future fitness, we require a situation in which future fitness varies among subordinates independently of the other parameters in the model (i.e. $r$, $c$, $b$ and $q$). Just such a situation commonly arises in nature when animals form a hierarchy or queue to inherit the position of the dominant (Field *et al.* 1999; Monnin & Ratnieks 1999; Kokko *et al.* 2001). In this case, the expected future fitness of a subordinate will vary systematically with her rank or position in the queue.

If we extend our two-player model to examine the influence of future fitness in multiplayer queues (see Appendix A), we obtain the results shown in figure 1. Two main predictions are evident: (i) for a given group size, both $\hat{h}_{\mathrm{sub}}$ and $\hat{h}_{\mathrm{dom}}$ are lower for higher-ranking subordinates. That is, subordinates should work less hard the closer they are to inheriting the position of dominant; and (ii) subordinates of a given rank should work less hard in larger groups because the pay-off from inheriting dominance is greater in larger, more productive groups.

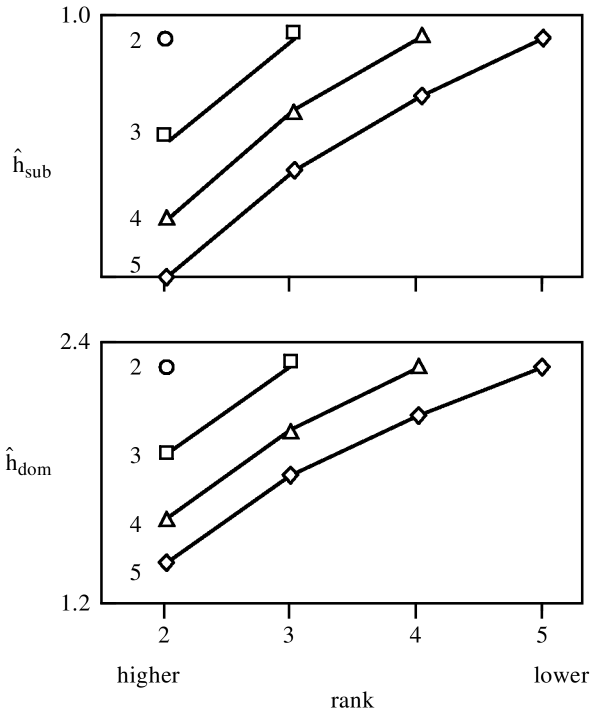

Figure 1. Evolutionarily stable levels of help from the perspectives of a subordinate ($\hat{h}_{\mathrm{sub}}$) and a dominant ($\hat{h}_{\mathrm{dom}}$), as a function of the inheritance rank of the subordinate. Numbers on the left-hand side of the graph indicate group size. Note the difference in scale on the $y$-axis in the two graphs. The solutions were obtained using numerical methods in the MATHEMATICA software package (MATHEMATICA 2.2, Wolfram Research). Other parameters: $b = 1$, $q = 1$, $c = 0.4$, $r = 0.5$ and $g = 0.5$.

## 3. AN EXPERIMENTAL TEST: HELPING EFFORT AMONG PAPER WASP CO-FOUNDRESSES

We tested the predictions in §2 on subordinate co-foundresses of the paper wasp *Polistes dominulus* in southern Spain (Conil de la Frontera, Cadiz, Spain, 36°15′N, 06°10′W). Paper wasps fit the assumptions of the model quite closely. Nests are founded each spring on the undersides of vegetation by groups of 1–10 mated foundresses, mainly relatives (Queller *et al.* 2000). The foundresses on each nest form a dominance hierarchy in which usually only the rank 1 female lays eggs (Turillazzi & Pardi 1977; Reeve 1991; Queller *et al.* 2000). Subordinate foundresses help by foraging for insect prey with which to feed the brood of the dominant female. As in other social insects (Schmid-Hempel & Wolf 1988; O'Donnell & Jeanne 1992), foraging is probably the costliest task undertaken by helpers. Co-foundresses are of similar age and so they are likely to have similar life expectancies (before taking into account the risks associated with helping). As assumed by our model, productivity (number of cells) increases linearly with group size ($n = 66$ nests, $r = 0.94$, $p < 0.0001$). The possibility of inheritance might have an important effect on the behavioural decisions of subordinates: 4 out of 20 dominants on unmanipulated multiple foundress nests disappeared over 40 days, or *ca*. 66% of the pre-worker period (see also Queller *et al*. 2000).

Our field study consisted of two stages. First, we measured helping effort by subordinates, then we carried out a removal experiment to identify the inheritance ranks of the individuals whose effort had been measured. The methods used in each stage are detailed in § 4.

## 4. METHODS

### (a) *Estimating helping effort*

We measured helping behaviour in a total of 41 multiple-foundress nests found on hedges of *Opuntia* cactus. Twenty-one of these nests were used in the experiment to test the predictions of the model, whereas the remaining 20 nests remained unmanipulated throughout and were used to estimate the survival costs of helping. All the nests had been located between 21 February and 8 March 2000 in a 100 m × 200 m area of pasture. After the discovery of a nest, we captured and individually marked all the wasps in the group with unique colour combinations of enamel paint spots on the thorax (e.g. Field *et al*. 1999, 2000), and measured their wing lengths using digital calipers. We determined group membership by a census of all nests every 5–8 days early in the morning before activity began.

Helping effort was measured over a 2 week period before worker emergence when all nests contained a mixture of small and large larvae. Our index of helping effort was the proportion of time that subordinates spent off the nest foraging. From 13 to 26 March 2000 (hereafter referred to as the 'helping period') we measured time off the nest for each group member by conducting repeated daytime censuses of all nests. Daytime censuses (average three censuses per day; intercensus interval, 45 min–1 h) were carried out on eight sunny afternoons (21–24 °C) between 12.00 and 17.00, the time when foraging is most frequent. Wasps that were alive (as determined by subsequent early morning censuses) but off the nest for a daytime census were assumed to be foraging. We classed as dominant those wasps that were present on the nest for more than 70% of daytime censuses (mean time on nest of dominants ± s.e. = 86.6 ± 0.03%). This criterion identified a single dominant in 20 out of 21 nests. In the remaining nest, two wasps were present for more than 70% of the time and we labelled as dominant the individual that was on the nest the most.

### (b) *Identifying inheritance ranks*

After helping effort had been measured as the proportion of time on the nest, inheritance ranks were identified from the sudden decrease in time off the nest by a new dominant after the previous dominant had been removed. After the helping period, we removed the original (rank 1) dominant foundress from the 21 experimental nests. Starting the next day, we made repeated daytime censuses of the nests for 3 days or more (minimum 15 censuses) and identified new dominants as the wasps (one per nest) that increased their time on the nest more than the 70% criterion described above. In practice, the new dominant was easy to identify because only one individual per nest markedly changed its behaviour after the removal. For example, the mean time on the nest for replacement dominants was 93.1 ± 0.02% (mean ± s.e.), compared with 40.0 ± 4% for the same individuals before the removals. By contrast, all other group members continued foraging at levels comparable to those before the removals (mean time on the nest in the 3 days after removals for other group members = 38.1 ± 3.6%).

Once identified, the replacement dominants (the rank 2 females) were removed from each nest and the nests again censused repeatedly for 3 days or more to identify the next wasps to inherit dominance (i.e. the rank 3 females). The process was repeated until only two wasps remained on the nest (and therefore no further removals were required to identify their relative ranking), or until the rank 5 female had been identified. The first removals of dominants were carried out on 27 March 2000 and the last on 22 April 2000. Most removals were completed before worker emergence, but in two nests the last removals were carried out a few days after workers had appeared.

### (c) *Statistics*

Analyses were done using generalized linear modelling in the GLMSTAT 4.0.3 package (Beath 1999), after the methods of Crawley (1993) and assuming binomial or normal errors as appropriate. In each analysis, we first fitted potential explanatory variables and their pairwise interactions. Starting with the interactions, we subtracted terms from the model until further removals led to significant ($p < 0.05$) increases in deviance, as assessed from tabulated values of $F$ with normal errors or $\chi^2$ with binomial errors (Crawley 1993). We report significance levels for terms when adding them last to this minimal adequate model.

To determine whether time off the nest entailed survival costs, we used the 20 unmanipulated multiple-foundress nests. From our daytime censuses, we estimated time off the nest during the helping period. Then we tested its effect on subsequent survivorship until 22 April using early morning and daytime censuses in a mark–release–recapture model that allowed for individual differences in re-sighting probability (Field *et al*. 1999, 2000). In the analysis of time off the nest versus the number of brood, we looked at the effect of the total number of cells (which is highly correlated with the number of brood: $r = 0.97$, $p < 0.0001$), as of 27 March, on the number of wasps off the nest during 10 daytime censuses over the preceding 4 days, controlling for group size. Means are quoted ± standard error.

## 5. RESULTS

Time off the nest varied widely between subordinates (16–94%). Wasps that spent more time off the nest had lower survivorship ($G_1 = 6.81$, $p < 0.01$, excluding dominants). Controlling for group size, subordinates in nests that contained more brood spent more time out of the nest ($\chi^2_1 = 9.073$, $p < 0.01$), as expected if this time represents primarily foraging. There was no relationship between rank and body size ($F_{4,65} = 0.59$, $p = 0.67$). Nest identity was initially included in this analysis, but its effect was not significant.

Our main results were clear-cut (figure 2). Both inheritance rank and group size had significant effects on the proportion of time that subordinates were absent from the nest during the helping period (rank: $\chi^2_1 = 25.68$, $p < 0.0001$; group size: $\chi^2_1 = 27.45$, $p < 0.001$). As predicted by our model, lower-ranked foundresses spent more time off the nest than higher-ranking individuals and foundresses of given rank foraged less in larger

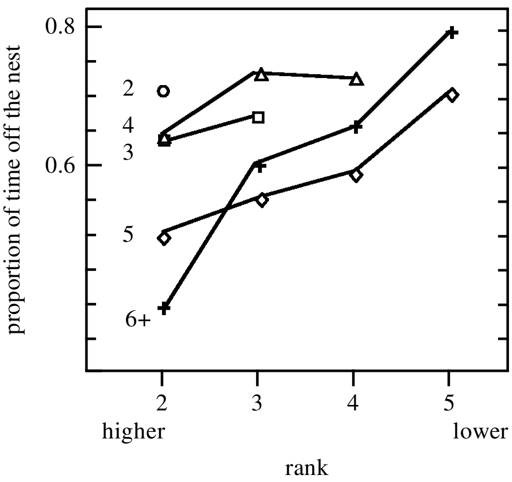

Figure 2. Proportion of daytime censuses in the helping period for which subordinates were absent (presumed foraging), as a function of their inheritance ranks. Numbers on the left-hand side of the graph indicate group size. Sample sizes: group size 2 (seven nests); 3 (two nests); 4 (five nests); 5 (two nests); and 6 + (five nests).

groups. The interaction between rank and group size was also significant ($\chi^2_{22} = 49.53$, $p < 0.001$) when added to a model that contains just the main effects. Dominants were excluded from the analysis and one other covariate tested (developmental stage of the oldest brood) did not have a significant effect. The same effects (rank and group size) remained significant whether the proportion of censuses off the nest was treated as a binomial variable or (to counter possible problems with non-independence of censuses) as an arcsine-transformed percentage. In addition, the Spearman rank correlation coefficient for subordinate rank versus time off the nest was positive (or, in two cases, zero) in 12 out of 14 nests in our sample that had more than two subordinates (binomial test: $p = 0.02$).

## 6. DISCUSSION

We attribute our results to variation among subordinates in the future component of fitness, as the other parameters in the model ($c$, $b$, $q$ and $r$) are unlikely to vary systematically with rank or group size. All subordinates are the same sex and of similar age, and there was no relationship between inheritance rank and body size. The energetic costs and mortality risks ($c$) associated with foraging are unlikely to vary with subordinate rank or group size, whereas the main benefits per unit effort (determined by $b$ and $q$ in the model) will be set by the encounter rate with prey. There is no evidence that relatedness ($r$) is correlated with group size (Queller *et al.* 2000) or rank, and foundresses probably do not discriminate relatedness among nest-mates (Queller *et al.* 1990; Keller 1997; Strassmann *et al.* 1997).

Our model should apply widely across cooperative animal societies, but most empirical studies have involved animals of unknown inheritance rank. Others have focused on variation in relatedness as a possible explanation for variation in helping effort with mixed results (see Clutton-Brock *et al.* (2000) and references therein). In several Hymenoptera, there is evidence that subordinates with higher inheritance ranks spend less time foraging off the nest (Gadagkar 1987; Chandrashekara & Gadagkar 1992; Ratnieks & Reeve 1992). In naked mole-rats, older, larger subordinates that are more likely to inherit the breeding position work less hard (Reeve 1992). In other cooperatively breeding birds and mammals, older subordinates often work harder than their younger counterparts (Heinsohn & Cockburn 1994; Sherman 1995; Komdeur 1996; Langen & Vehrencamp 1999). This pattern might arise because helping is more costly for younger subordinates (Heinsohn & Cockburn 1994; Boland *et al.* 1997; Heinsohn & Legge 1999). In terms of our model, the effect of future fitness is confounded by age-related changes in the cost of help $c$. To further test our model, experiments are required using animals of known inheritance rank that are able to control for potential confounding variables.

The model makes several simplifying assumptions. For instance, the productivity that subordinates stand to inherit is a function of group size only, rather than individual or collective helping effort. It is possible, however, that individuals who help, reap the benefits of inheriting a larger or more productive group in the future (Clutton-Brock *et al.* 2000; Kokko *et al.* 2001). It would be interesting to incorporate such 'group augmentation' effects in the current model as these might be expected to counter or ameliorate the costs of helping that drive our results. Nevertheless, the close match between our theoretical and empirical results suggests that the trade-off between current and future fitness captures a fundamental cause of variation in helping effort. This conclusion adds to the growing recognition that the current versus future trade-off can have a strong influence on other social attributes, such as reproductive skew (Kokko & Johnstone 1999; Ragsdale 1999) and aggression (Enquist & Leimar 1990).

Whether work rate is primarily under the control of the dominant or the subordinates themselves does not affect our two main predictions and will often remain unclear. However, the contrasting effects of relatedness on $\hat{h}_{\text{sub}}$ and $\hat{h}_{\text{dom}}$(see expressions (2.5) and (2.6)) indicate a simple test to distinguish which individual is in control, at least in species in which animals can respond to differences in relatedness among group members (Reeve 1992; Emlen 1997).

We thank Andrew Bourke, Rufus Johnstone, Istvan Karsai, Hanna Kokko and two anonymous referees for comments on the manuscript. Gavin Shreeves wrote the program to analyse mark–recapture data and helped with our analysis of survivorship. Financial support was provided by a Natural Environment Research Council research grant to J.F.

## APPENDIX A: A MULTIPLAYER MODEL

Consider a queue of $n$ individuals comprising a single dominant and ($n$–1) subordinates at ranks 2, 3, ... $n$. If all the individuals in a group have the same average lifespan (before taking into account the costs associated with helping), the probability of a subordinate at rank $j$ reaching the position of dominant is $1/j$ (Field *et al.* 1999). Let the total productivity of the group increase linearly with group size at rate $g$, where $g$ is a constant (similar results are obtained if we assume that productivity increases with group size at an accelerating, or decelerating, rate). The expected future fitness ($w_0$) of an individual of rank $j$ in a group of size $n$ is now given by $w_0 = \ (gn)/\text{j}$. Substituting this expression for $w_0$ into equation (2.3) in § 2, we can write the future direct fitness of a rank $j$ subordinate as a function of her own helping effort as

$$w_j(h_j) = (gn/j)(1 - ch_j). \qquad \text{(A 1)}$$

Now, the inclusive fitness pay-off to a subordinate who lies at rank $j$, in terms of her own helping effort $h_j$ and the helping efforts of all the other members of the group $h_i$ ($i = 2, \ldots n, ij$) can be written

$$W_{\text{sub}j}(h_j) = w_j(h_j) + r\left[k(h_j) + \sum_{\substack{i=2\\ i\neq j}}^{n} w_i(h_i)\right]. \qquad \text{(A 2)}$$

We seek a set of evolutionarily stable helping efforts $\{\hat{h}_2$ $\hat{h}_3, \hat{h}_4, \ldots\}$ where each $\hat{h}_j$ maximizes the inclusive fitness pay-off of the subordinate at rank $j$ in the hierarchy (given by equation (A 2)), taking into account the helping effort of the other members of the group.

We illustrate how to solve the model with an example (see also Houston & Davies 1985). Consider a group of four individuals: one dominant and three subordinates. Starting with the rank 2 subordinate, we substitute our expressions for $w_2(h_2)$, $w_3(h_3)$ and $w_4(h_4)$ into (A2) to yield $W_{\text{sub2}}(h_2)$ in terms of $h_2$, $h_3$ and $h_4$. Expressions for $W_{\text{sub3}}(h_3)$ and $W_{\text{sub4}}(h_4)$ in terms of $h_2$, $h_3$ and $h_4$ are obtained in the same fashion. The evolutionarily stable levels of help for each subordinate are found by solving the simultaneous equations

$$(\delta W_{\text{sub2}}(h_2))/\delta h_2 = 0,$$
$$(\delta W_{\text{sub3}}(h_3))/\delta h_3 = 0,$$
$$(\delta W_{\text{sub4}}(h_4))/\delta h_4 = 0,$$

for $h_2$, $h_3$ and $h_4$. (We also need to verify that the solutions reflect a stable, fitness-maximizing equilibrium; Houston & Davies 1985) The set of solutions $\{\hat{h}_{\text{sub2}}, \hat{h}_{\text{sub3}}, \hat{h}_{\text{sub4}}\}$ represents the combination of helping efforts for which the inclusive fitness of each subordinate is maximized, given the effect of her decision on the effort of the others.

By the same method, we can find the best arrangement of helping effort from the perspective of the dominant. The inclusive fitness pay-off of the dominant that is associated with the helping effort of the rank $j$ subordinate is given by

$$W_{\text{dom}j}(h_j) = k_j(h_j) + r\left(\sum_{i=2}^{n} w_i(h_i)\right),$$

and the solutions $\{\hat{h}_{\text{dom2}}, \hat{h}_{\text{dom3}}, \text{etc.}\}$ are obtained by simultaneously maximizing the expressions $W_{\text{dom}j}(h_j)$ with respect to $h_j$ for $j = 2, \ldots n$.

## REFERENCES

Beath, K. J. 1999 GLMSTAT, v. 4.0.3. Available from kjbeath@kagi.com.

Boland, C. R. J., Heinsohn, R. & Cockburn, A. 1997 Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. *J. Anim. Ecol.* **66**, 683–691.

Chandrashekara, K. & Gadagkar, R. 1992 Queen succession in the primitively eusocial tropical wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *J. Insect Behav.* **5**, 193–209.

Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A. D. C., McIlrath, G., Chadwick, P., Brotherton, P. N. M., O'Riain, J. M., Manser, M. & Skinner, J. D. 1999 Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. Lond.* B **265**, 185–190.

Clutton-Brock, T. H., Brotherton, P. N. M., O'Riain, M. J. & Griffin, A. S. 2000 Individual contributions to babysitting in a cooperative mongoose *Suricata suricatta*. *Proc. R. Soc. Lond.* B **267**, 301–305.

Crawley, M. J. 1993 *GLIM for ecologists*. Oxford: Blackwell Scientific.

Emlen, S. T. 1991 Evolution of cooperative breeding in birds and mammals. In *Behavioural ecology: an evolutionary approach*, 3rd edn (ed. J. R. Krebs & N. B. Davies), pp. 301–337. Oxford, UK: Blackwell Scientific.

Emlen, S. T. 1997 Predicting family dynamics in social vertebrates. In *Behavioural ecology: an evolutionary approach*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 228–253. Oxford: Blackwell Scientific.

Enquist, M. & Leimar, O. 1990 The evolution of fatal fighting. *Anim. Behav.* **39**, 1–9.

Field, J., Shreeves, G. & Sumner, S. 1999 Group size, queuing and helping decisions in facultatively eusocial hover wasps. *Behav. Ecol. Sociobiol.* **45**, 378–385.

Field, J., Shreeves, G., Sumner, S. & Casiraghi, M. 2000 Demographic advantages in the evolution of eusociality. *Nature* **404**, 869–871.

Gadagkar, R. 1987 Social structure and the determinants of queen status in the primitively eusocial wasp *Ropalidia cyathiformis*. In *Chemistry and biology of social insects* (ed. J. Eder & H. Rembold), pp. 377–378. Munich: J. Peperny.

Hamilton, W. D. 1964 The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* **7**, 1–52.

Heinsohn, R. & Cockburn, A. 1994 Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proc. R. Soc. Lond.* B **256**, 293–298.

Heinsohn, R. & Legge, S. 1999 The cost of helping. *Trends Ecol. Evol.* **14**, 53–57.

Houston, A. I. & Davies, N. B. 1985 The evolution of cooperation and life history in the dunnock, *Prunella modularis*. In *Behavioural ecology: the ecological consequences of adaptive behaviour* (ed. R. M. Sibly & R. H. Smith), pp. 471–487. Oxford: Blackwell Scientific.

Keller, L. 1997 Indiscriminate altruism: unduly nice parents and siblings. *Trends Ecol. Evol.* **12**, 99–103.

Kokko, H. & Johnstone, R. A. 1999 Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. R. Soc. Lond.* B **266**, 571–578.

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond.* B **268**, 187–196.

Komdeur, J. 1996 Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behav. Ecol.* **7**, 326–333.

Langen, T. A. & Vehrencamp, S. L. 1999 How white-throated magpie-jay helpers contribute during breeding. *Auk* **116**, 131–140.

Monnin, T. & Ratnieks, F. L. W. 1999 Reproduction versus work in queenless ants: when to join a hierarchy of hopeful reproductives? *Behav. Ecol. Sociobiol.* **46**, 413–422.

O'Donnell, S. & Jeanne, R. L. 1992 Lifelong patterns of forager behaviour in a tropical swarm-founding wasp: effects of specialization and activity level on longevity. *Anim. Behav.* **44**, 1021–1027.

Queller, D. C., Hughes, C. R. & Strassmann, J. E. 1990 Wasps fail to make distinctions. *Nature* **344**, 388.

Queller, D. C., Zacchi, F., Cervo, R., Turillazzi, S., Henshaw, M. T., Santorelli, L. A. & Strassman, J. E. 2000 Unrelated helpers in a social insect. *Nature* **405**, 784–787.

Ragsdale, J. E. 1999 Reproductive skew extended: the effect of resource inheritance on social organization. *Evol. Ecol. Res.* **1**, 859–874.

Ratnieks, F. L. W. & Reeve, H. K. 1992 Conflict in single-queen hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. *J. Theor. Biol.* **158**, 33–65.

Reeve, H. K. 1991 *Polistes*. In *The social biology of wasps* (ed. K. Ross & R. Matthews), pp. 99–148. Ithaca, NY: Cornell University Press.

Reeve, H. K. 1992 Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature* **358**, 147–149.

Schmid-Hempel, P. 1990 Reproductive competition and the evolution of work load in social insects. *Am. Nat.* **135**, 501–526.

Schmid-Hempel, P. & Wolf, T. 1988 Foraging effort and life span of workers in a social insect. *J. Anim. Ecol.* **57**, 500–521.

Seger, J. 1991 Cooperation and conflict in social insects. In *Behavioural ecology: an evolutionary approach*, 3rd edn (ed. J. R. Krebs & N. B. Davies), pp. 338–373. Oxford: Blackwell Scientific.

Sherman, P. T. 1995 Social organisation of cooperatively polyandrous white-winged trumpeters (*Psophia leucoptera*). *Auk* **112**, 296–309.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.

Strassmann, J. E., Klingler, C. J., Arevalo, E., Zacchi, F., Husain, A., Williams, J., Seppa, P. & Queller, D. C. 1997 Absence of within-colony discrimination in behavioural interactions of swarm-founding wasps. *Proc. R. Soc. Lond.* B **264**, 1565–1570.

Turillazzi, S. & Pardi, L. 1977 Body size and hierarchy in polygynic nests of *Polistes gallicus* (L.) (Hymenoptera Vespidae). *Monitore Zool. Ital.* **11**, 101–112.

West-Eberhard, M. J. 1981 Intragroup selection and the evolution of insect societies. In *Natural selection and social behaviour: recent research and new theory* (ed. R. D. Alexander & D. W. Tinkle), pp. 3–17. New York: Chiron.