

Original Article

Do paper wasps negotiate over helping effort?

Lynda Donaldson,^a Faye J. Thompson,^a Jeremy Field,^b and Michael A. Cant^a^aCentre for Ecology and Conservation, University of Exeter, Cornwall Campus, Treliever Road, Penryn, Cornwall TR10 9EZ, UK and ^bSchool of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

Received 21 April 2013; revised 15 August 2013; accepted 15 August 2013; Advance Access publication 4 October 2013

Recent theory and empirical studies of avian biparental systems suggest that animals resolve conflict over parental care via a process of behavioral negotiation or “rules for responding.” Less is known, however, about whether negotiation over helping effort occurs in cooperatively breeding animal societies or whether behavioral negotiation requires a relatively large brain. In this study, we tested whether negotiation over help occurs in a social insect, the paper wasp *Polistes dominulus*, by recording individual responses to both observed and experimentally induced foraging returns by other group members. In our experiments, we manipulated food delivery to the nest in 2 ways: 1) by catching departing foragers and giving them larval food to take back to the nest and 2) by giving larval food directly to wasps on the nest, which they then fed to larvae, so increasing food delivery independently of helper effort. We found no evidence from Experiment 1 that helpers adjusted their own foraging effort according to the foraging effort of other group members. However, when food was provided directly to the nest, wasps did respond by reducing their own foraging effort. One interpretation of this result is that paper wasp helpers adjust their helping effort according to the level of offspring need rather than the work rate of other helpers. Negotiation based on indicators of demand rather than work rate is a likely mechanism to resolve conflict over investment in teams where helpers cannot observe each other’s work rate directly, as is commonly the case in insect and vertebrate societies.

Key words: cooperative breeding, foraging, helping effort, negotiation, paper wasp, *Polistes dominulus*, provisioning.

INTRODUCTION

In more than 80% of bird species, both mothers and fathers contribute to the rearing of young (Cockburn 2006). The fitness pay-offs of parents are positively correlated (because of their shared genetic interest in the success of their offspring), but (except in the case of obligate monogamy) each parent would prefer their mate to work harder than that mate’s own optimum work rate (Chase 1980; Houston and Davies 1985). How will this evolutionary conflict over parental investment be resolved? The first formal models to investigate this question assumed that parents make a single, fixed decision over the level of investment, often referred to as a “sealed bid” (Chase 1980; Houston and Davies 1985; Schwagmeyer et al. 2002). The models predicted that biparental care is evolutionarily stable (ES) if mutations leading to reduced effort in one player select for mutations in the other player, which partially compensate for this reduction.

McNamara et al. (1999) noted that this approach is limited because it assumes that all members of a particular sex are identical and prohibits partners from responding in real, behavioral time to variation in their partner’s work rate. To address these limitations, McNamara et al. (1999, 2003) extended the basic framework of models on biparental care to include a phase of behavioral “negotiation” between parents, prior to allocation of investment.

Rather than solving for an ES fixed effort level, this model solves for the ES “rule for responding” to the effort of varied partners. Different partners invest at different levels according to their underlying “quality,” that is, the cost they pay for a given level of effort. What the ES rule specifies is how “responsive” a player should be to changes (in real time) in the effort of its partner. The prediction that partners should partially compensate for changes in each other’s behavior still holds in this model (Schwagmeyer et al. 2002), but the predicted effort levels are lower than in the sealed bid model, and offspring generally end up worse off overall. In some cases, offspring may even be better off with a single parent rather than 2 negotiating ones (McNamara et al. 2003).

Experimental studies have supported the assumption of negotiation models that parents respond in behavioral time to changes in the effort of their partner (Wright and Cuthill 1989, 1990; Markman et al. 1995; Sanz et al. 2000; Hunt and Simmons 2002; Smiseth and Moore 2004; Lendvai et al. 2009). However, the responses of parents to manipulation of their partner’s effort range from partial and full compensation to no change (Whittingham et al. 1994; Schwagmeyer et al. 2002; Suzuki and Nagano 2009). Some studies have even revealed a matching response by partners, a result not predicted by either sealed bid or negotiation models (Hinde 2006). Effort matching can be explained, however, if parents are uncertain about the precise level of offspring need and use the effort level of their partner to estimate this (Johnstone and Hinde 2006). Incorporating uncertainty into models of parental

Address correspondence to M.A. Cant. E-mail: m.a.cant@exeter.ac.uk.

investment may help to explain the diverse results of experimental studies in avian biparental care systems (Hinde and Kilner 2007).

Modeling conflict over investment becomes more complex in cooperatively breeding groups where helpers assist parents with parental care (Hårdling et al. 2003; Carranza et al. 2008; Savage et al. 2013). In this case, helpers and parents may both benefit when other group members supply a greater level of care, but the payoffs of investment will depend on the number of carers, patterns of relatedness within groups, and reproductive value of offspring (Hatchwell and Russell 1996; Hårdling et al. 2003). Kin selection models have been developed to explain how selection acts on helping strategies and the causes of individual variation in helping effort; but again, most of these models adopt the sealed bid approach (e.g., Cant and Field 2001; Kokko et al. 2001; Hamilton and Taborsky 2005; Carranza et al. 2008). Here too, experimental studies have shown that parents and helpers do respond in a variety of different ways to the presence and efforts of others, some demonstrating a compensatory response (Komdeur 1994; Hatchwell 1999; Langen and Vehrencamp 1999; Wright and Dingemanse 1999; Legge 2000; Bergmüller and Taborsky 2005), whereas others were recorded to maintain their level of care (Emlen and Wrege 1991) or even increase their parental effort when helpers were present (Valencia et al. 2006). Johnstone (2011) highlighted the lack of negotiation models of helping effort and addressed this shortfall by extending the biparental model of McNamara et al. (1999) to the case of a pair with a single helper. Stable response rules in this case can lead to “load lightening” by helpers, that is, for parents to ease off and let helpers do much of the work. The general prediction of this model is that helpers and breeders should be most responsive to changes in each other’s effort where the cost of investment is linear or gently accelerating, and least responsive where costs sharply accelerate with investment level (Johnstone 2011). The specific predictions of this model have yet to be tested in cooperative vertebrates. To our knowledge, there have been no tests of the assumptions or predictions of negotiation models in cooperative insects.

Here, we test the main assumptions of sealed bid and negotiation models in cofoundress associations of the cooperatively breeding paper wasp *Polistes dominulus*. Specifically, we use provisioning experiments and observational foraging data to test whether paper wasps respond on a behavioral timescale to changes in foraging effort and the rate of food delivery to the nest. Evidence that wasps change their foraging rate in response to changes in the helping behavior of their nest mates would suggest that sealed bid models do not apply to this system and would lend support for negotiation approaches to the study of conflict over helping effort (McNamara et al. 1999, 2003; Johnstone and Hinde 2006; Johnstone 2011; Lessells and McNamara 2012). Conversely, if helping effort is unresponsive to changes in the provisioning behavior of social partners, sealed bid models may provide a simple general framework to understand variation in individual helping effort and overall group productivity in cooperatively breeding insects.

Note that this is a system in which the main cost of helping is predation risk, and helping costs are expected to increase more or less linearly with foraging effort (Cant and Field 2001). Thus, according to Johnstone’s (2011) model, the system is favorable to the evolution of responsiveness. However, it is less clear whether the system fits some of the informational assumptions of negotiation models. In particular, it is unclear whether wasps could detect changes in the effort level of their group members because they cannot assess comings and goings from the nest while they are themselves foraging. It may be, therefore, that wasps use some other

cue to assess the current or historical provisioning effort of their groupmates, such as offspring size or need (Lessells and McNamara 2012). We test this hypothesis by manipulating foraging behavior and offspring hunger independently.

METHODS

Study area and population

The study was conducted during March and April 2011 on farmland and pasture close to Conil de la Frontera, Cadiz, Southern Spain (see Cant and Field 2001; Shreeves et al. 2003; Cant, English, et al. 2006; Cant, Llop, et al. 2006; Leadbeater et al. 2011). We first located nests of *P. dominulus* consisting of 3–11 foundresses on hedges of *Opuntia* cactus. All group members were captured in the morning (when it was too cold for the wasps to fly) and individually marked using unique color combinations of enamel paint applied to the thorax (Cant and Field 2001). We censused nests in the early morning and repeatedly during daytime foraging sessions to establish group membership and to identify dominant individuals, following the methodology of previous studies (Cant and Field 2001; Cant, Llop, et al. 2006).

Measurement of foraging behavior

Throughout the warmest part of the day (1100–1700 hours), subordinate foundresses regularly leave the nest on foraging trips in the meadowland that surrounds the *Opuntia* hedges. The target prey is insect larvae (primarily Lepidoptera, Coleoptera, and Diptera), although wasps also leave the nest to find water and wood pulp for nest construction. Live prey are located on host plants using visual and olfactory cues, pounced on, and killed by biting (reviewed by Richter 2000). The prey is masticated into a small ball of meat approximately 0.1–0.4 cm across, a process called malaxation. The malaxated food is carried back to the nest and provisioned to larvae in their cell. Large balls of food may be divided and fed to several larvae in turn.

We videotaped foraging behavior by foundresses on dry, warm days between 30 March and 26 April 2011, prior to the emergence of workers. On the day of video recording, all nests were mapped and censused for eggs and larvae. Offspring in each cell were categorized as eggs, small larvae, medium larvae, large larvae, or pupae, depending on their size and color (Field et al. 2000; Shreeves et al. 2003). Because we were interested in foraging and provisioning of larvae, we excluded early-stage nests that contained less than 2 medium-sized larvae. Previous work has shown that more foraging occurs once groups have reached this stage and groups are also more likely to be stable, with less chance of unmarked wasps joining the nest. Temperature was recorded throughout the study period using Tinytag Transit 2 data loggers (Alana Ecology Ltd, UK) placed next to nests. Nests were filmed using digital camcorders mounted on tripods.

We used observational foraging data and 2 experimental manipulations to test whether cofoundresses adjust their foraging effort according to the foraging effort of their nest mates. This yielded 3 classes of data, which are described in detail below. We analyzed each class of data using a within-nest design in which we compared behavior in a 20-min “control” period with a 20-min “treatment” period recorded from the same nest on the same day (see also Lendvai et al. 2009). This within-nest design meant that each nest acted as its own control and helped to control for potentially confounding variables such as weather, location or orientation of the nest, stage of development, and group size.

Observational data

A total of 20 nests were filmed for a 2-h period without disturbance to determine how wasps respond to the return of another group member with food. Within this section of film, the 20-min period following the return of a single foundress with food (a “return period”) was chosen and compared with another, random 20-min period on that nest on the same day, which acted as a “control period.” In order to control for temporal variation, the control period occurred after the return period in 10 nests and before the return period in the remaining 10 nests. The time between control and return periods ranged from 12 min to 3 h 10 min.

Experiment 1: wasp provisioning

The aim of this experiment was to test how foundresses on the nest responded to the return of a forager while controlling for possible confounding factors in the observational foraging data, such as the type of prey item returned, or how long it took for the forager to find the piece of food. We captured departing foundresses in a butterfly net as they left the nest and provided each with a small piece of waxworm from forceps. Once the wasp grasped the food, she was released from the net and allowed to return to the nest. Each nest was filmed for the 20-min period immediately before (control) and after (treatment) the return of the focal wasp with food. One trial was performed on each of 19 nests. In 2 cases, the provisioned wasp did not return within 2 h, and these were excluded from the analysis.

Experiment 2: nest provisioning

The aim of this experiment was to test whether group members responded to changes in the amount of food delivered to the nest, independently of any change in foraging behavior. We provisioned 1 foundress on the nest directly with a small section of larval food (waxworm; Lepidoptera) using long handled forceps. The food was slowly moved toward 1 foundress on the nest who reached out to take it from the forceps. Food was presented when at least 2 wasps were present so that we could measure the response of the wasp that did not receive the food. Nests were filmed for the 20-min period immediately before this food was presented (control) and for the 20 min after (treatment). One trial was performed on each of 19 nests. In 3 cases, the experiment was abandoned due to poor weather, leaving 16 nests in the analysis. To check that responses to the experiment were due to the provisioning of food rather than human disturbance, we carried out a “control disturbance,” which involved leaning into the nest and pushing a stick toward it without food. Sixteen nests were filmed for 20 min following this control disturbance compared with an undisturbed 20-min period in the same filming session.

Video analysis

Videos were analyzed using VLC media player (version 1.1.11). We analyzed in detail behavioral responses to a foraging event (either the return of a forager or an act of nest provisioning) in the short term (the period 2 min after the foraging event) or the longer term (the period 20 min after the event). The arrival and departure time of all wasps to and from the nest were recorded to the nearest second; departure rate was used as an index of foraging effort given that wasps have to leave the nest in order to forage (Reeve and Gamboa 1987). A wasp was counted as having departed the nest if it had left the field of view for more than 1 min, because many wasps leave the nest briefly (for less than 1 min) to defend their nest from wasps and other insects that approach too closely.

The mean number of wasps on the nest was calculated for both the 2- and 20-min sections during the control and observation periods of all 3 classes of data. Following Reeve and Gamboa (1987), we calculated 2 measures of foraging activity: 1) total departure rate (TDR), a group measure of the total number of departures during the observation periods (2 or 20 min) and 2) individual departure rate (IDR), the average individual foraging effort, calculated as TDR divided by the mean number of wasps on the nest during the period of observation (either 2 or 20 min). All our analyses used IDR as the response variable because this measure captures both the number of individuals that could have left within each period and the number that did leave. Dominant foundresses were included in the calculation of IDR along with lower ranked foundresses. We calculated IDRs both including and excluding the focal wasp that returned with or was provided with food to determine whether statistical differences between control and treatment periods were attributable to changes in the behavior of the focal wasp or to its fellow group members. We denote these measures the “IDR_{All}” and the “IDR_{Others},” respectively. The only exception to this was the wasp provisioning experiment (Experiment 1), where IDR_{All} could not be calculated for the control period immediately before the return of the provisioned wasp because she was in our butterfly net for all or part of this period. We used this rather indirect method to test the impact of the focal wasp so that we were unconstrained in our selection of the control period (e.g., we did not need to ensure that the control period started with an unsuccessful return of the focal wasp with food).

Statistical analyses

Data analysis was conducted in the statistical software package R version 2.12.0. Models were tested in a stepwise backward manner, beginning with the maximum model containing all terms and removing nonsignificant interactions, followed by the main terms, until further removal caused a significant decrease in the explanatory power of the model ($P < 0.05$). All statistical values included in the report were obtained from the minimum adequate model.

During data analysis, it became apparent that very few wasps left within the immediate 2-min period in all data sets. To cope with potential problems of this zero inflated data, we used generalized linear mixed effects models with binomial error structure, using lmer in the lme4 R package, to test whether the probability of any wasps leaving within this short time was any different between the control and return periods. The 2-min period for each nest was scored with a 1 (if any wasps did leave) or a 0 (when no wasps left). The chance of a wasp leaving was included as the response variable, with observation period (before/after) as a fixed effect and nest included as a random effect, because each nest was monitored twice. In this 2-min data, we focused exclusively on nonfocal wasps only (IDR_{Others}) because the focal wasp was handling or processing food for some of this short period. All other analyses were conducted using data obtained for the 20-min observation period.

We tested whether returns with food (from both observational data and Experiment 1) or the provisioning of food to the nest (Experiment 2) affected foraging behavior using linear mixed effect models (LME) with observation period (before/after the return/manipulation) as a fixed effect and IDR as the response variable. As the 2 observation periods compared were collected from the same nest, nest identity was included as a random effect. Where we had measures for both IDR_{All} and IDR_{Others}, it was possible to determine the influence of the behavior of our focal wasp on the

overall departure rate of the nest, within a given period. This effect was also analyzed using LME, with IDR in the after/before period as the response variable, whether the focal wasp was included or excluded from this measure as a fixed term, and nest as a random effect.

Model simplification for all mixed models was performed using maximum likelihood, and model checks were formed from the minimum restricted maximum likelihood model (Crawley 2005). Response variables were square-root ($\sqrt{\cdot}$) transformed in some analyses, where errors were nonnormal. All statistical values obtained from the LME analyses are reported as likelihood ratio (L), which closely matches the χ^2 distribution, where the degrees of freedom (ν) is the difference in the number of parameters between the 2 models compared (with and without the term tested).

RESULTS

Lack of an immediate response

The probability of any of the group members leaving within the 2-min observation period was not significantly different between the control and return/after period for observational data, nor the 2 experiments (LME—observational data: $\chi_1^2 = 0.80$, $P = 0.37$, $N = 20$; wasp provisioning experiment: $\chi_1^2 = 0.37$, $P = 0.54$, $N = 17$; nest provisioning experiment: $\chi_1^2 = 1.19$, $P = 0.27$, $N = 16$). There was, therefore, no evidence that other wasps responded within 2 min 1) to the return of foundresses from observational foraging trips and from trips where they had been provisioned with waxworm (Experiment 1) nor 2) to the provision of waxworm to the nest (Experiment 2). All our subsequent analyses focus on the longer term responses to foraging events, that is, the 20-min period after a foraging event.

Response to the return of a wasp from an observed foraging trip

Over the 20-min period following the return of a wasp from a successful foraging trip, other group members were not significantly more likely to depart from the nest compared with the control period, although there was a trend in this direction (IDR of other foundresses [IDR_{Other}] in control vs. return periods—LME with $\sqrt{\cdot}$ transformed response variable: $L_1 = 3.21$, $P = 0.073$; Figure 1). This pattern was more pronounced when we included the focal wasp in the calculation of IDR: IDR_{All} was significantly higher in the return period than 1) IDR_{All} in the control period (LME with $\sqrt{\cdot}$ transformed response variable: $L_1 = 4.81$, $P = 0.028$; Figure 1) and 2) the IDR of other foundresses in the return period (IDR_{Other}) (LME with $\sqrt{\cdot}$ transformed response variable: $L_1 = 5.53$, $P = 0.019$; Figure 1). Together these results suggest that, on unmanipulated nests, 1) other foundresses were not statistically more likely (at a significance level of $P = 0.05$) to leave the nest following the return of a nest mate with food and 2) a forager returning with food is more likely than other foundresses to itself leave again within 20 min.

Experiment 1: response to the return of an experimentally provisioned wasp

Other foundresses were not more likely to depart the nest after the return of a provisioned wasp than during the 20-min period immediately before this return (LME with $\sqrt{\cdot}$ transformed response variable: $L_1 = 0.53$, $P = 0.47$). IDR after the return of the focal wasp was not significantly different when the focal wasp was included

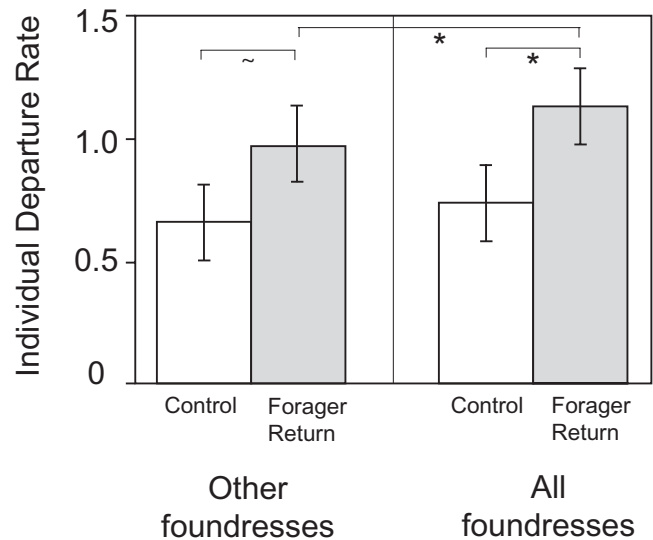


Figure 1

The Individual Departure Rate (IDR) of wasps in a randomly selected “control” period versus a “return” period (i.e., the 20 min after the return of a wasp with food) on unmanipulated nests. IDR is a measure of individual foraging effort. The left-hand panel shows the IDR calculated for other foundresses on the nest, excluding the focal wasp that returned (referred to as IDR_{Other} in the text); the right-hand panel shows the IDR calculated for all foundresses, including the focal wasp (referred to as IDR_{All} in the text). Bars show raw means \pm standard errors (SE). * $P < 0.05$; $\sim P = 0.07$. $N = 20$ nests.

or excluded in the calculation of IDR (IDR_{All} vs. IDR_{Other}; LME with $\sqrt{\cdot}$ transformed response variable: $L_1 = 3.04$, $P = 0.082$). The direction of this result was that IDR_{All} was marginally higher than IDR_{Other}. These results suggest that the capture and provision of food to a focal wasp did not lead to changes in the subsequent foraging behavior of either that focal individual or the other wasps on the nest.

Experiment 2: response to the provision of food at the nest

Excluding the wasp that received the piece of waxworm while on the nest, the IDR of other wasps was significantly lower in the 20-min period after the food was provided than before (IDR_{Other}, before vs. after; LME: $L_1 = 4.78$, $P = 0.029$). Departure rate was also lower when the wasp that received the food was included in the analysis, but at borderline significance level (IDR_{All}, before vs. after; LME: $L_1 = 3.72$, $P = 0.054$). Both IDR_{All} and IDR_{Other} were not significantly different in the 20-min period following a control disturbance compared with an undisturbed 20-min period in the same filming session (IDR_{All}; LME: $L_1 = 0.062$, $P = 0.80$; IDR_{Other}; LME with $\sqrt{\cdot}$ transformed response variable: $L_1 = 3.17$, $P = 0.075$).

Because food provided to the nest can take up to 2 min to masticate and deliver to larvae, we repeated our analysis excluding the first 2 min of the 20-min observation period after the manipulation and compared with the 2- to 20-min period prior to provisioning, to account for the possibility that constraints associated with processing food could have affected the original conclusion. The results were qualitatively similar: the other group members were less likely to leave in the 2- to 20-min period after food was provided than the 2- to 20-min period before (LME: $L_1 = 4.10$, $P = 0.043$; Figure 2) and the result for all foundresses (including the foundress who obtained the food) revealed no significant difference between

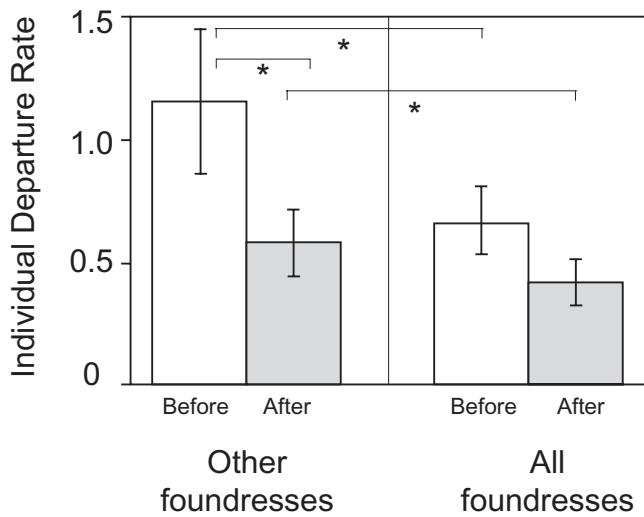


Figure 2

The IDR of wasps for the 2- to 20-min period before and after the nest was provisioned with larval food (Experiment 2). The left-hand panel shows the IDR_{Others} , excluding the wasp that took the food from the forceps; the right-hand panel shows IDR_{All} including the wasp that took the food. Bars show raw mean \pm SE. * $P < 0.05$. $N = 16$ nests.

the before/after observation periods (LME: $L_1 = 2.89$, $P = 0.089$; Figure 2). Finally, the mean IDR_{All} was significantly lower than the mean IDR_{Others} in the 2- to 20-min period before (LME with \sqrt transformed response variable: $L_1 = 5.71$, $P = 0.017$) and 2- to 20-min period after (LME: $L_1 = 11.11$, $P < 0.001$) provisioning, suggesting that the wasp that received food was less likely than the other wasps to leave the nest in both of these time periods. Together, these results suggest that 1) focal wasps that received food may have been individuals with particularly low probability of departure; these focal wasps were less likely than other group members to depart in the 20 min after the foraging event (taking into account the time required to masticate and deliver food) and 2) other foundresses reduce their foraging effort after the delivery of food to the nest, independently of any change in foraging behavior of nest mates.

DISCUSSION

We found that foundresses were not significantly more likely to leave the nest after an observed foraging return or after an experimentally induced foraging return. However, direct provisioning of larval food to a focal wasp on the nest caused other foundresses to reduce their foraging effort, suggesting that wasps do respond in real time to food availability on the nest or larval hunger. The relatively weak response of other foundresses to wasp foraging returns may mean that foundresses pay relatively little attention to each other's foraging activity, as assumed by sealed bid models, or that their decisions form part of a more complex negotiation process to that modeled by McNamara et al. (1999, 2003) and Johnstone (2011). For example, foundresses may respond to the state of offspring or their level of need rather than solely to the work rate of their social partners (Johnstone and Hinde 2006; Lessells and McNamara 2012). We discuss these possibilities below.

Our results suggest that wasps do not adjust their foraging effort to changes in the foraging effort or success per se of other group members. It could be that our experimental handling of wasps

resulted in deviant behavior of the returning forager and obscured some underlying responsiveness. However, previous studies of this system (Shreeves et al. 2003) and of tropical hover wasps (Field et al. 2000) also found that removing a forager from the group had no effect on the foraging effort of remaining group members. The failure to detect any major response of nest mates to changes in foraging effort in the short term (this study) or the long term (Shreeves et al. 2003) is consistent with the assumptions of simple sealed bid models of parental care (Chase 1980; Houston and Davies 1985; Hinde 2006; Johnstone and Hinde 2006). However, it contrasts with field studies of birds, where experimental changes in the effort of one partner are often found to influence the effort of the other (e.g., Markman et al. 1995; Wright and Dingemanse 1999; Sanz et al. 2000; Hinde 2006). Why do some species exhibit real-time responsiveness, whereas others apparently do not? A plausible explanation for the lack of response to changes in foraging effort in this system is that wasps probably have very limited ability to monitor directly the foraging behavior of their social partners. The negotiation models of McNamara et al. (1999, 2003) and Johnstone (2011) assume that foraging individuals have complete information about the work effort of their social partners. In some species, this may be a plausible assumption: for example, foraging birds can communicate during their foraging trips (Hinde 2006) and monitor the nest visits of their mate. In *P. dominulus*, however, groups commonly consist of 4 or more foundresses (Zanette and Field 2008, 2009) and foragers spend 50–94% of the time off the nest (Cant and Field 2001). In this system, it is difficult to see how foundresses could reliably monitor each other's foraging efforts directly (although conceivably this information could be communicated by the dominant, because she is almost always on the nest).

In contrast to the lack of response to the experimentally induced return of a focal wasp with food, providing food directly to a wasp on the nest did lead to a reduction in the departure rate of other wasps on the nest. Thus, one explanation for this result is that foundress foraging decisions are tuned primarily to the hunger levels of larvae, rather than foraging effort per se. However, if larval hunger were the only factor on which wasps based their decisions, we might also expect wasps to be less likely to leave after an observed foraging return, because this also results in larvae receiving food, whereas in fact our results suggest a trend toward the opposite pattern: wasps were somewhat *more* likely to leave after the delivery of food by a returning forager (Figure 1).

How are we to explain these different responses to the delivery of food by a forager versus the delivery of food without the return of a forager? In addition to information gleaned from their own foraging success, wasps could base their foraging decisions on 2 other sources of information, the foraging success of other wasps (which could provide information of how successful foraging trips are likely to be at that time) and the level of offspring hunger (which could provide information of how valuable to the offspring a foraging trip would be at that time). Our data suggest that wasps give weight to the latter source of information but not the former. In hover wasps (*Liostenogaster flavolineata*) and paper wasps (*P. dominulus*), groups that are experimentally reduced in size (by removing a subordinate foundress) respond by biasing their provisioning toward more developed larvae (Field et al. 2000; Shreeves et al. 2003). Thus, it appears that wasps do monitor larval state and can adjust their care accordingly. In several cooperatively breeding birds and mammals, both parents and helpers respond to the level of need of their brood (Wright 1998; MacGregor and Cockburn 2002; Bell 2008; Manser et al. 2008; McDonald et al.

2009). Where foraging effort is difficult to monitor directly (e.g., in social insects and large groups of cooperative breeders), offspring hunger or state is likely to be a more reliable source of information on which to base foraging decisions than the behavior of other investors.

Theoretical models to date have not considered negotiation in larger social groups such as those of *P. dominulus*. The model by Johnstone (2011), for example, focuses on the interaction between 3 players. Extensions to larger groups and to social hierarchies may be necessary to understand negotiation over care in cooperative breeders. For example, in *P. dominulus* and the tropical hover wasp *L. flavolineata*, lower ranked foundresses spend more time off the nest than those of higher rank, most likely because they have less to lose (in terms of future direct fitness) than higher ranked nest mates (Cant and Field 2001, 2005; Field et al. 2006). Our finding that wasps returning from an observed foraging trip were more likely to depart again compared with their nest mates is consistent with this finding and suggests that the wasps we were most likely to observe returning with food were lower ranked, hardworking foragers.

To conclude, our observational and experimental data suggest that paper wasps do not negotiate over helping effort in the manner assumed by most current theoretical models (McNamara et al. 1999, 2003; Johnstone 2011). Rather, individual wasps appear to adjust their foraging behavior primarily according to current offspring state. This does not mean that sealed bid models are appropriate to understand the coevolution of foraging strategies or that wasps are blindly unresponsive to changes in the investment levels of their partners. Rather, it suggests that wasps may be involved in a negotiation in which the primary source of information used in investment decisions is the level of need or state of offspring. This source of information reflects current and historical investment and is more accessible to foundresses than information derived from direct observations of partner effort. Negotiation based on cues from offspring need has recently been modeled by Lessells and McNamara (2012) who assume that parents engage in repeated bouts of investment and decide at each time step how much to invest based on the current size of offspring, which reflect the joint history of investment by both parents. Extension of this approach to cooperative systems would be particularly interesting. Further theoretical work would also help to understand the social and ecological conditions, or features of basic biology, which determine which sources of social information can be accessed or utilized in biparental and cooperative groups. Empirically, manipulations of offspring hunger (e.g., by larval or chick feeding experiments) together with manipulation of forager or parental effort would help tease apart the sources of information used in negotiation of family conflicts.

Handling editor: Bob Wong

REFERENCES

- Bell MBV. 2008. Strategic adjustment of begging effort by banded monogoose pups. *Proc R Soc B Biol Sci.* 275:1313–1319.
- Bergmüller R, Taborsky M. 2005. Experimental manipulation of helping in a cooperative breeder: helpers ‘pay to stay’ by pre-emptive appeasement. *Anim Behav.* 69:19–28.
- Cant MA, English S, Reeve HK, Field J. 2006. Escalated conflict in a social hierarchy. *Proc R Soc B Biol Sci.* 273:1471–2954.
- Cant MA, Field J. 2001. Helping effort and future fitness in cooperative animal societies. *Proc R Soc Lond Ser B Biol Sci.* 268:1959–1964.
- Cant MA, Field J. 2005. Helping effort in a dominance hierarchy. *Behav Ecol.* 16:708–715.
- Cant MA, Llop JB, Field J. 2006. Individual variation in social aggression and the probability of inheritance: theory and a field test. *Am Nat.* 167:837–852.
- Carranza J, Polo V, Valencia J, Mateos C, de la Cruz C. 2008. How should breeders react when aided by helpers? *Anim Behav.* 75:1535–1542.
- Chase I. 1980. Cooperative and non-cooperative behavior in animals. *Am Nat.* 115:827–857.
- Cockburn A. 2006. Prevalence of different modes of parental care in birds. *Proc R Soc B Biol Sci.* 273:1375–1383.
- Crawley MJ. 2005. *Statistics: an introduction using R.* Chichester (UK): John Wiley and Sons.
- Emlen ST, Wrege PH. 1991. Breeding biology of white-fronted bee-eaters at Nakuru—the influence of helpers on breeder fitness. *J Anim Ecol.* 60:309–326.
- Field J, Cronin A, Bridge C. 2006. Future fitness and helping in social queues. *Nature.* 441:214–217.
- Field J, Shreeves G, Sumner S, Casiraghi M. 2000. Insurance-based advantage to helpers in a tropical hover wasp. *Nature.* 404:869–871.
- Hamilton IM, Taborsky M. 2005. Unrelated helpers will not fully compensate for costs imposed on breeders when they pay to stay. *Proc R Soc B Biol Sci.* 272:445–454.
- Hårdling R, Kokko H, Arnold KE. 2003. Dynamics of the caring family. *Am Nat.* 161:395–412.
- Hatchwell BJ. 1999. Investment strategies of breeders in avian cooperative breeding systems. *Am Nat.* 154:205–219.
- Hatchwell BJ, Russell AF. 1996. Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus*: an experimental study. *Proc R Soc Lond Ser B Biol Sci.* 263:83–88.
- Hinde CA. 2006. Negotiation over offspring care?—a positive response to partner-provisioning rate in great tits. *Behav Ecol.* 17:6–12.
- Hinde CA, Kilner RM. 2007. Negotiations within the family over the supply of parental care. *Proc R Soc B Biol Sci.* 274:53–60.
- Houston AI, Davies NB. 1985. The evolution of cooperation and life history in the dunnock *Prunella modularis*. In: Sibly RM, Smith RH, editors. *Behavioural ecology: ecological consequences of adaptive behaviour.* Oxford: Blackwell Scientific Publications.
- Hunt J, Simmons LW. 2002. Behavioural dynamics of biparental care in the dung beetle *Onthophagus taurus*. *Anim Behav.* 64:65–75.
- Johnstone RA. 2011. Load lightening and negotiation over offspring care in cooperative breeders. *Behav Ecol.* 22:436–444.
- Johnstone RA, Hinde C. 2006. Negotiation over offspring care—how should parents respond to each other’s efforts? *Behav Ecol.* 17:818–827.
- Kokko H, Johnstone RA, Clutton-Brock TH. 2001. The evolution of cooperative breeding through group augmentation. *Proc R Soc Lond B Biol Sci.* 268:187–196.
- Komdeur J. 1994. Experimental-evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behav Ecol Sociobiol.* 34:175–186.
- Langen TA, Vehrencamp SL. 1999. How white-throated Magpie-Jay helpers contribute during breeding. *Auk.* 116:131–140.
- Leadbeater E, Carruthers JM, Green JP, Rosser NS, Field J. 2011. Nest inheritance is the missing source of direct fitness in a primitively eusocial insect. *Science.* 333:874–876.
- Legge S. 2000. Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. *Anim Behav.* 59:1009–1018.
- Lendvai ÁZ, Barta Z, Chastel O. 2009. Conflict over parental care in house sparrows: do females use a negotiation rule? *Behav Ecol.* 20:651–656.
- Lessells CM, McNamara JM. 2012. Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proc R Soc B Biol Sci.* 279:1506–1514.
- MacGregor NA, Cockburn A. 2002. Sex differences in parental response to begging nestlings in superb fairy-wrens. *Anim Behav.* 63:923–932.
- Manser MB, Madden JR, Kunc HP, English S, Clutton-Brock T. 2008. Signals of need in a cooperatively breeding mammal with mobile offspring. *Anim Behav.* 76:1805–1813.
- Markman S, Yom-tov T, Wright J. 1995. Male parental care in the orange tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. *Anim Behav.* 50:655–669.
- McDonald PG, Kazem AJN, Wright J. 2009. Cooperative provisioning dynamics: fathers and unrelated helpers show similar responses to manipulations of begging. *Anim Behav.* 77:369–376.
- McNamara JM, Gasson CE, Houston AI. 1999. Incorporating rules for responding into evolutionary games. *Nature.* 401:368–371.

- McNamara JM, Houston AI, Barta Z, Osorno JL. 2003. Should young ever be better off with one parent than with two? *Behav Ecol.* 14:301–310.
- Reeve HK, Gamboa GJ. 1987. Queen regulation of worker foraging in paper wasps: a social feedback control system. *Behaviour.* 102:147–167.
- Richter MR. 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu Rev Entomol.* 45:121–150.
- Sanz J, Kranenbarg S, Tinbergen J. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). *J Anim Ecol.* 69:74–84.
- Savage JL, Russell AF, Johnstone RA. 2013. Maternal costs in offspring production affect investment rules in joint rearing. *Behav Ecol.* 24:750–758.
- Schwagmeyer PL, Mock DW, Parker GA. 2002. Biparental care in house sparrows: negotiation or sealed bid? *Behav Ecol.* 13:713–721.
- Shreeves G, Cant MA, Bolton A, Field J. 2003. Insurance-based advantages for subordinate co-foundresses in a temperate paper wasp. *Proc R Soc Lond B Ser Biol Sci.* 270:1617–1622.
- Smiseth PT, Moore AJ. 2004. Behavioral dynamics between caring males and females in a beetle with facultative biparental care. *Behav Ecol.* 15:621–628.
- Suzuki S, Nagano M. 2009. To compensate or not? Caring parents respond differentially to mate removal and mate handicapping in the burying beetle, *Nicrophorus quadripunctatus*. *Ethology.* 115:1–6.
- Valencia J, De La Cruz C, Carranza J, Mateos C. 2006. Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. *Anim Behav.* 71:1021–1028.
- Whittingham LA, Dunn PO, Robertson RJ. 1994. Female response to reduced male parental care in birds: an experiment in tree swallows. *Ethology.* 96:260–269.
- Wright J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. *Behav Ecol Sociobiol.* 42:423–429.
- Wright J, Cuthill I. 1989. Manipulations of sex differences in parental care. *Behav Ecol Sociobiol.* 25:171–181.
- Wright J, Cuthill I. 1990. Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. *Behav Ecol.* 1:116–124.
- Wright J, Dingemanse NJ. 1999. Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Anim Behav.* 58:345–350.
- Zanette L, Field J. 2009. Cues, concessions, and inheritance: dominance hierarchies in the paper wasp *Polistes dominulus*. *Behav Ecol.* 20:773–780.
- Zanette LRS, Field J. 2008. Genetic relatedness in early associations of *Polistes dominulus*: from related to unrelated helpers. *Mol Ecol.* 17:2590–2597.