Polistes nest founding behavior: a model for the selective maintenance of alternative behavioral phenotypes

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Starks, P. T. & Fefferman, N. H. 2006: *Polistes* nest founding behavior: a model for the selective maintenance of alternative behavioral phenotypes. — *Ann. Zool. Fennici* 43: 456–467.

Here we present a novel model for the selective maintenance of alternative phenotypes. Our model is appropriate for systems where the expression of alternative tactics is both condition and frequency dependent. We use *Polistes dominulus* as our model system, and show how frequencies of solitary nest founding, collaborative nest founding, usurpation of defended nests, and adoption of abandoned nests are predicted to vary with changes in ecological and social conditions. To accomplish this we (1) review commonly used models that explain the selective maintenance of alternative phenotypes, (2) describe some basic life-history characteristics of *Polistes* wasps, (3) present a novel condition dependent mixed strategy model, (4) use this model to predict frequencies of alternative tactics under conditions of differing survivability, relatedness between co-foundresses, and reproductive skew between co-foundresses, and (5) provide future directions for refining and testing this unifying model.

Introduction

Natural selection is the cornerstone of research in the field of animal behavior, whether the research is on proximate mechanisms or on ultimate causations. It is intuitive to assume the result of natural selection on a given variant within a population of variants to be an eventual population consisting of a single, most reproductively successful variant (Reeve & Sherman 1993). Many populations, however, are characterized by stable variant subsets (*see* Gross 1996, Plaistow *et al.* 2004). Satellite and calling males in some toads (Leary *et al.* 2005), territorial and sneaker males in gobys (Scaggiante *et al.* 2005), and tending and coursing males in feral goats (Saunders *et al.* 2005) are just a few examples where alternative behavioral traits are maintained in a population. Accordingly, there has been significant research effort to produce models describing the selective maintenance of these alternatives (*see* Plaistow *et al.* 2004). These models can be described as either frequency or condition dependent (*see* Gross 1996). Our goal is to combine these complementary approaches into a single, theoretical model and to test this novel model on the paper wasp *Polistes dominulus*.

Current models of the selective maintenance of alternative phenotypes

Gross (1996) provided a logical framework for understanding how natural selection can main-
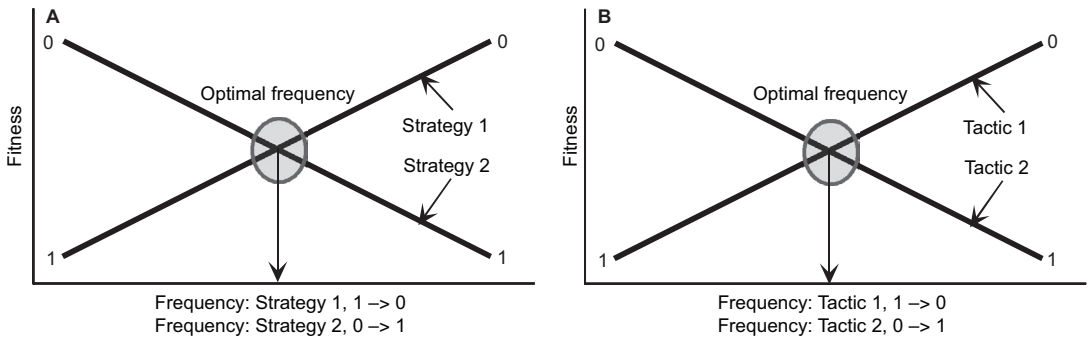
Fig. 1. — **A**: A hypothetical description of a genetically polymorphic population where genetic differences give rise to different strategies. When the fitness of each strategy is negatively frequency-dependent on the other strategy, the population will reach an equilibrium point for the *average* fitness payoff. — **B**: A hypothetical description of a population where genetic differences do not give rise to different tactics, but individuals rather can perform one of two discreet behaviors (tactics). When the fitness of each tactic is negatively frequency dependent on the other tactic, the population will reach an equilibrium point for the *average* fitness payoff.

tain alternative behavioral phenotypes within a given population (*see* also Dominey 1984, and Austad 1984). Within the general framework of mating behavior, Gross described alternative strategies (i.e., genetic polymorphisms), mixed evolutionary strategies, and conditional strategies. In this framework, a tactic is a phenotype that arises from a strategy, and a strategy is a genetic program (Gross 1996).

If a population is comprised of individuals displaying different tactics, and each tactic is specific to a single strategy, the population is then best described by an alternative strategy model (i.e., a genetically polymorphic system). In this system, an individual can perform only one tactic regardless of context. To be selectively maintained, the tactics must have negatively frequency dependent fitnesses that intersect at an intermediate frequency (Fig. 1A). A common example of an alternative strategy system is sex in sexually reproducing animals, where the sex ratio describes the optimum frequencies of the alternative tactics (i.e., male and female).

Mixed evolutionary strategies and conditional strategies, alternatively, are not considered underlain by genetic differences. Accordingly, we assume that all possible tactics can arise from a single genetic strategy (Gross 1996). The characteristics that distinguish between mixed and conditional strategies are the probabilities of tactic expression, and their respective fitness payoffs. A population engaged in a mixed strategy, defined

by two tactics, contains multiple individuals performing tactics with a certain probability. As in the case described as an alternative strategy, these tactics must have negatively frequency dependent fitnesses to be selectively maintained (Maynard Smith 1982; *see* Fig. 1B).

Conditional strategies are characterized by individuals adopting the tactic that has the highest payoff based on the individual's current condition (Gross 1996). Condition-based alternative phenotypes are expected to have a switchpoint — a game theoretic equilibrium — where the fitness payoff for either tactic is identical. As opposed to the systems where tactic expression is frequency dependent, in this system individuals are expected to display the tactic that has the highest average fitness payoff (Fig. 2). It is believed that alternative reproductive phenotypes (e.g., mate acquisition) are likely to be different tactics in a conditional strategy for most populations (Gross 1996, Kain 1999, but *see* Plaistow *et al*. 2004).

Alternative phenotypes in *Polistes* wasps

During the colony founding period, *Polistes* foundresses display several different forms of nest founding behavior (*see* Reeve 1991, Turillazzi & West-Eberhard 1996). Spring foundresses may initiate colonies alone, form associations with other females, usurp established conspecific
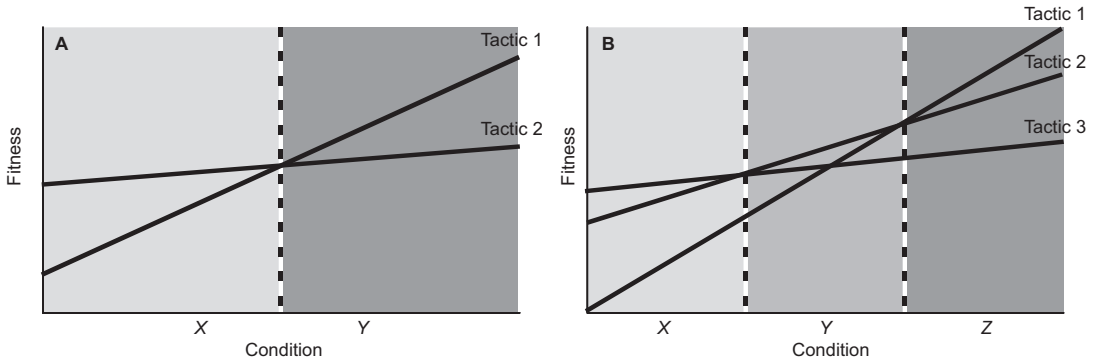
Fig. 2. — **A**: A hypothetical description of a conditional strategy with two possible tactics. At conditions in the X range, tactic 2 (light gray) has a higher expected fitness payoff than tactic 1 (dark gray). However, at conditions in the Y range, tactic 1 has the higher expected fitness payoff. Since animals are expected to maximize their fitness, all animals within condition range X will play the light gray tactic whereas all animals within condition range Y will play the dark gray tactic. — **B**: An extension of the two tactic strategy to include a third tactic. Tactic 3 (light gray) has the highest fitness payoff for animals of condition *X*, tactic 2 (gray) has the highest fitness payoff for animals of condition *Y*, and tactic 1 (dark gray) has the highest fitness payoff for animals of condition *Z*. Following the same logic as above, animals within a given condition range will perform the behavior that has the highest expected fitness payoff.

colonies, or even 'sit-and-wait' to adopt abandoned nests. Females that adopt abandoned nests may have left multiple-foundress associations (Nonacs & Reeve 1993), lost their colonies due to predation or other forms of damage (Cervo & Dani 1996), or waited to adopt an orphaned nest instead of initiating one (Nonacs & Reeve 1993, Starks 1998, 2001).

Within an enclosure, it has been shown that the *P. dominulus* females who engage in the sit-and-wait reproductive tactic adopt the most mature nests (Starks 1998, 2001, *see* also Nonacs & Reeve 1993) and prefer orphaned nests with a large number of fourth and fifth instar larvae. Data indicate that adopters are less cooperative than nest initiators, prefer mature nests to nests with a higher likelihood of kinship, and conserve energy during the nest founding period (Starks 2001). As with cases of usurpation (Klahn 1988), once adoption occurs, adopters destroy the previous foundress' eggs and early instar larvae and replace them with their own eggs; older larvae and pupae are allowed to complete development (Starks 1998).

Polistes wasps as a model system

Polistes are ideal for modeling the selective maintenance of alternative phenotypes because — unlike long-lived animals — lifetime reproductive success can be easily estimated via nest cell counts. In addition, techniques used for basic genetic analyses have been well worked out (*see* Strassman *et al*. 1996), the animals seem to behave naturally when maintained in enclosure populations (*see* Starks 1998, 2001, 2003), the behavioral tactics in question are reasonably discrete (*see* West Eberhard 1969, Reeve 1991), and all activity can be easily observed on the unenveloped nest.

Since some *P. dominulus* individuals express multiple behaviors within their lifetime (Starks 2001), it does not appear that nesting behavior in *P. dominulus* can be described by an alternative strategy model (i.e., arising from a genetic polymorphism). Because nesting behavior in *P. dominulus* does not appear to be underlain by genetic differences, nesting behavior is likely to be best described by a genetically monomorphic model where multiple potential options (tactics) are available to each foundress. Because usurper and adopter wasps conserve energy during the founding period, and because their success is dependent on finding a colony before the worker period begins, this nesting option is conditional — and based not only on relative status but also on time. Because the collaborative strategies are dependent on finding a collaborator with whom to found a nest, their success will be mutually

All possible conditions within a population

Fig. 3. — **A**: Representation of the condition-dependent fitness of individuals within a population. In this population there are three possible conditions; *X, Y* & *Z*. — **B**: An enlargement of condition *Y*. Here we see that two different tactics are performed by individuals within this condition. — **C**: The likelihood of an individual of *condition Y* performing tactic 1 or tactic 2 is dependent on the frequencies of each. Since the fitness of each tactic is negatively frequency dependent, the population will settle into an equilibrium frequency of individuals playing either tactic.
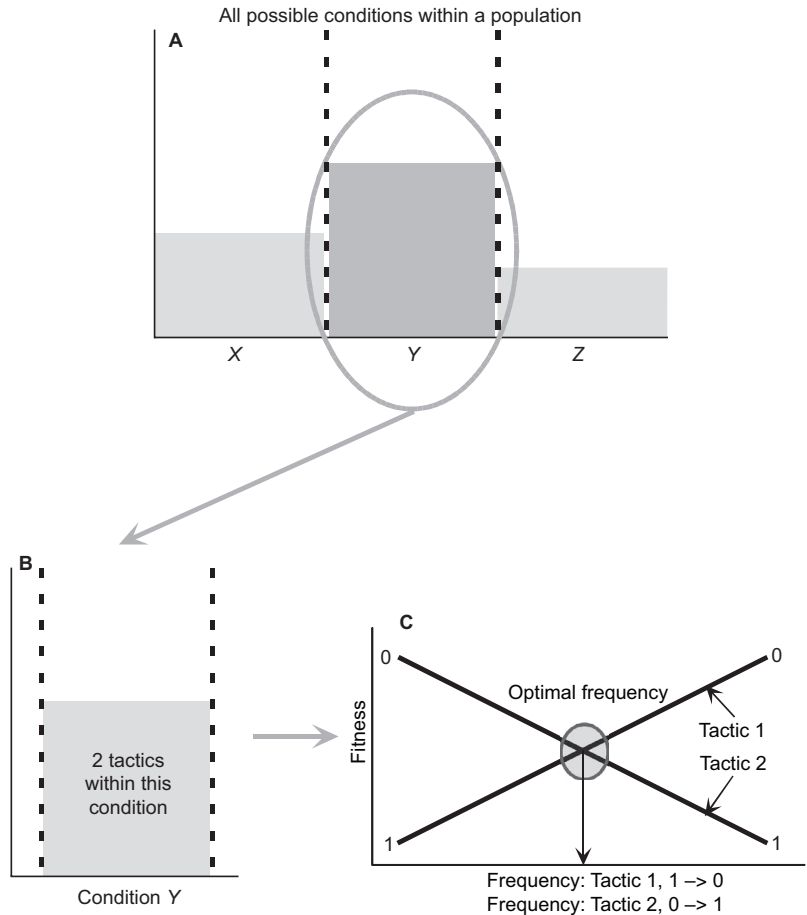
frequency dependent. Finally, because the sit-and-wait tactic is dependent on the presence of a significant single foundress population, its success will also be frequency dependent. As such, to properly model this system we will need a condition dependent mixed strategy model.

Condition dependent mixed strategy

Here we present the verbal and graphical logic behind a condition dependent mixed strategy. A condition dependent mixed strategy model assumes that multiple tactics are available to an individual, that the expression of the tactics is condition dependent, and the expected fitness payoff of any one tactic is dependent on the frequency of other tactics expressed by other individuals of a similar condition (Fig. 3).

The model

To create a predictive model of phenotypic frequency, we have built a game theoretic model to evaluate the payoff for each of the behavioral tactics over time, relative to each other, and based on individual condition. Since our measure of selection is reproductive fitness, we measure this utility payoff by quantifying the relative reproductive success of each individual employing each tactic.

The expected payoff structure can be estimated both by incorporating the relative frequency of each, and the condition of each individual relative to an expected average. Relative frequency influences the level of competition (both direct and indirect) on the availability of resources remaining unexploited by others (or produced by others, in the case of adoption and

nest usurpation). Therefore, these frequencies impact the expected payoff for each tactic as an aggregate. Individual condition influences the expectation of success for each tactic relative to the condition of others as an estimation of success in competition. In this way, our model incorporates elements of each "pure" game to examine the more complicated payoff structure of condition dependent mixed evolutionary stable strategies.

Within the scope of our model, we examine the outcome of four behaviors: The Solitary Foundress, in which a female founds her own nest and tends it unassisted. The Multiple Foundress with two collaborative foundresses, in which a single nest is tended by dominant and subordinate females who have a skewed reproductive output. The Usurper, in which a female does not initiate a nest, but rather overthrows a single foundress from her nest. Finally, the Adopter, in which a female does not initiate a nest, but rather waits for the opportunity to adopt an orphaned nest.

Each of these behaviors is hypothesized to have a different expected payoff over time as environmental constraints shift, potentially altering both the relative frequencies of each tactic and the relative condition of individuals. For example, as the summer progresses, some of the Adopter females will have adopted orphaned nests. This will decrease the number of Adopters remaining who have yet to find a nest. Simultaneously, it is likely that predation by invertebrates (e.g., spiders) on single foundresses will continue to provide the same rate of nest availability, increasing the expectation of finding an available nest for adoption over time. In order to track these expected payoffs consistently and uniformly, all nests are assumed to be founded at the beginning of the summer, though they may change "ownership" at any time, and individuals are assumed to be able to accurately assess their own condition.

In this model, we focus on five basic components of wasp nesting ecology. We represent these components in terms of their impact on nest survival and reproductive contribution over time for each founding tactic. The magnitude of impact of each of these components can be determined empirically.

1. $F_a(t)$ = Probability of nest ownership over time: We define the probability of possessing a nest at a particular time t, given a particular founding tactic a. (Where $a \in$ {Solitary Foundress, Collaborative Dominant Foundress, Collaborative Subordinate Foundress, Usurper, and Adopter}.) Since a solitary or dominant foundress creates a nest independent of others, $F_{\text{Solitary Foundress}}(t)$ and $F_{\text{Dominant Foundress}}(t)$ are equal to 1. For a subordinate foundress, $F_{\text{Subordinate Foundress}}(t)$ is defined as the product of the probabilities of both finding a nest to join and being allowed to join it. For an 'opportunist' when a = Adopter or Usurper, $F_a(t)$ is the probability of either finding an abandoned nest, or finding a nest with a single foundress who can be ejected successfully. Note that in the cases of the subordinate foundress and the usurper, these probabilities will themselves be dependent on individual condition over time. In order to examine the expected frequencies of behavioral tactics, we assume that the population's distribution of individual condition is such that a potential usurper could expect an average of 1 in 10 nests to possess a single foundress whom the usurper could successfully depose. (This assumption can easily be altered for use in a different system, possibly also incorporating a probabilistic estimation of relative condition and pairwise encounters.)

2. Nest maturity over time: We define $X_a(t)$ = to the expected maturity of a nest, founded according to tactic a, at time t. These estimates can be made using an overall nest maturity score, which can be calculated for each nest (Pardi 1951; *see* Starks 1998, 2001). Based on field observations, we assume that the rate of maturation can be increased by the presence of a subordinate foundress. We similarly assume that an adopted nest has a slightly slower maturation after losing its original foundress due to a time gap between the loss and being tended by an adopting foundress. For simplicity, we assume an average state of maturity for all usurped and adopted nests (though this assumption can be relaxed).

3. Probability of nest survival: We define $S_a(X)$ = the probability of nest survival until worker

eclosion based on a particular stage of total nest maturity expected when the nest is founded under tactic *a*. This measure will be implicitly (rather than explicitly) dependent on time, since the stage of maturity is itself time dependent. Additionally, this metric will be specific to the founding tactic, therefore if a single foundress is deposed via usurpation, her nest will not be considered to have survived from the perspective of that single foundress. Therefore, the success of usurpers will contribute negatively to the probability of nest survival for nests with solitary foundresses. (Again, we assume that a usurper will not target nests with multiple foundresses.)

4. Expected reproduction: We define R_f = the percentage of reproduction expected to be attributed to each foundress (f) on the nest. (For example, for a solitary foundress nest, $R_{Solitary}$ = 1. Values for collaborating foundresses can vary significantly, sometimes as a function of relatedness [*see* Reeve *et al.* 2000, Nonacs *et al.* 2006].)

5. Potential size of a successful nest: We define N_a = the relative size to which a successful nest can grow when reared under the founding tactic *a*. Note that unlike the other components, this is not at all dependent on time. This will contribute both to the probability of overall nest survival and also to the probability of reproductive success gained by rearing this nest.

With these components, we can then construct an expression for the expected payoff for each tactic, over time:

$$P(t) = F_a(t)X_a(t)S_a(X_a(t))R_f N_a$$

With the payoff defined in this way, we are able to calculate baseline values that can be compared to different scenarios. For this paper, we limit these comparisons to situations of varying survivorship for solitary foundresses and for both solitary and subordinate foundresses, different values of relatedness between co-foundresses, and different values of reproductive skew between co-foundresses (Table 1). For values used in the Baseline Scenario, *see* Table 2.

Results

Baseline conditions

The data presented in Fig. 4 show the population level expected fitness payoffs for each tactic over time. At the population level, dominant foundresses and solitary foundresses are expected to perform well, with the expected payoff for subordinate foundresses and for usurping and adopting wasps to be significantly lower. Our payoff results indicate that the relationship between adopting and usurping is not constant, but rather adoption is expected to provide a higher payoff early and

Table 1. Scenarios investigated: Note that in order to represent relatedness and skew, the variable affected in both cases is R_f. The biological scenario is then integrated into the calculation of the appropriate values of R_f. For example, in Altered Scenario 3, the reproductive allotment on the nest was assumed to remain at 80% for the dominant and 20% for the subordinate, as in the Baseline Scenario. Therefore, a relatedness of 75% between the two foundresses would provide for the dominant foundress 100% relatedness to the 80% of eggs she had laid, and 75% relatedness to the eggs the subordinate had laid, yielding in total, 95% relatedness to the total reproductive output of the nest. Similar calculations yield an 80% relatedness for the subordinate foundress.

	Scenario concept	Values altered from baseline
Baseline scenario	Baseline	–
Altered scenario 1	Survivorship (solitary only)	High: $S_{Solitary}(X) := 1.5 S_{Solitary}(X)$ Low: $S_{Solitary}(X) := 0.5 S_{Solitary}(X)$
Altered scenario 2	Survivorship (solitary and subordinate)	High: $S_a(X) := 1.5 S_a(X)$ Low: $S_a(X) := 0.5 S_a(X)$ Where $a \in$ {Solitary or Subordinate}
Altered scenario 3	Relatedness	$R_{Primary}$ = 95%, $R_{Secondary}$ = 80%
Altered scenario 4	Skew	High: $R_{Primary}$ = 93%, $R_{Secondary}$ = 83% Low: $R_{Primary}$ = 70%, $R_{Secondary}$ = 30%
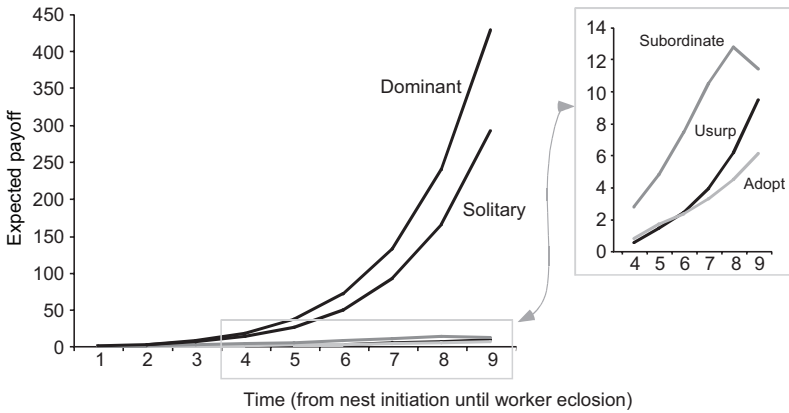
Fig. 4. The data presented are the population level expected fitness payoffs for each tactic. The blown up section on the right shows differences between subordinate, usurper, and adopter wasps. This general relationship is altered each time parameter values are changed.
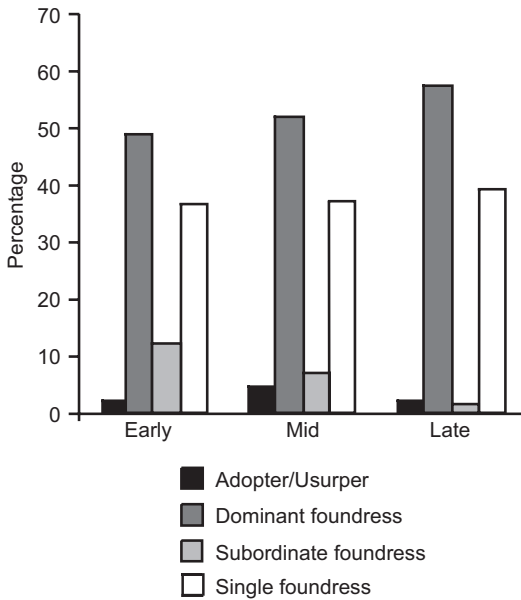
usurpation will be favored as the time to worker eclosion approaches (Fig. 4, close-up section).

These data can be transformed into frequencies, allowing for predictions regarding the frequency that we expect for each given tactic expressed in a population. Figure 5 shows the frequency results for the baseline scenario at three points during the founding period: early, mid, and late. While these frequencies sum to 100%, they only represent the predicted frequencies that wasps perform given tactics. Because the ability to be a dominant foundress on a mul-

Table 2. Values used in the Baseline Scenario. Note that the values used are only important as relative metrics and should be considered only as a measure of comparison against other values of the same variable for the other tactics. (Values below were informed by Reeve & Nonacs 1995, Starks 2001).

|	Time	Strategy (a)				
		Single foundress	Dominant foundress	Subordinate foundress	Usurper	Adopter
$S_a(X)$	All times	$(1 - N_{Usurp})0.94(1.25)^{X(t)}$	$2.0(1.25)^{X(t)}$	$2.0(1.25)^{X(t)}$	$(1.25)^{X(t)}$	$(1.25)^{X(t)}$
N_a	All times	0.6	1.0	1.0	0.6	0.6
R_f	All times	100%	80%	20%	100%	100%
$F_a(t)$	1	100%	47%	47%	1%	6%
	2	100%	47%	40%	2%	6%
	3	100%	47%	35%	3%	6%
	4	100%	47%	30%	4%	6%
	5	100%	47%	25%	5%	6%
	6	100%	47%	20%	6%	6%
	7	100%	47%	15%	7%	6%
	8	100%	47%	10%	8%	6%
	9	100%	47%	5%	9%	6%
	10	100%	47%	0%	10%	6%
	11	100%	47%	0%	0%	0%
$X_a(t)$	1	1	1	1	1	1
	2	2	2	2	2	2
	3	4	4	4	4	4
	4	6	6	6	6	6
	5	8	8	8	8	8
	6	10	10	10	9	9
	7	12	12	12	10	10
	8	14	14	14	11	11
	9	16	16	16	12	12
	10	18	18	18	13	13
	11	20	20	20	14	14

Fig. 5. The frequency distributions for each tactic under the baseline scenario at three points during the founding period: early, mid, and late. These frequencies represent the 'ideal game' for individuals in the population, however interests may not converge for all tactics (e.g., there may be fewer individuals willing to be subordinates than there are individuals who want a subordinate).

tiple foundress nest is dependant on the availability of a suitable subordinate, the frequency of multiply founded nests is expected to be the frequency of subordinate foundresses. The remaining fraction of dominant foundresses are hypothesized to appear in the natural setting as solitary foundresses.

Survivorship: constraints on solitary founding

The probability of survival for solitary foundresses can be elevated or depressed (Table 1; Altered Scenario 1). In this way, our model approximates a variable used in reproductive skew models: constraints on solitary founding (e.g., *see* Reeve & Keller 2001). As constraints on solitary founding increase, the amount of direct reproduction needed to make cooperation beneficial to a subordinate wasp should decrease. As such, one may predict that, in contexts where constraints on solitary founding are high, the rel-
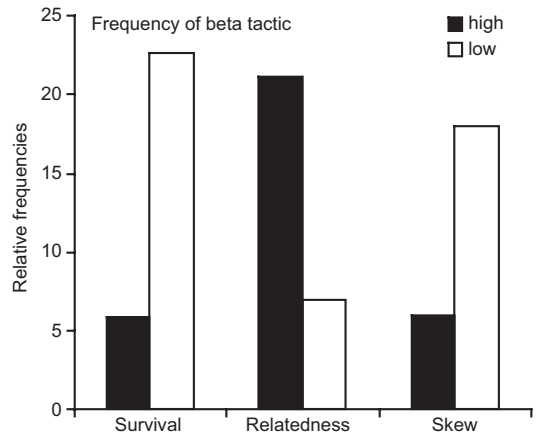
Fig. 6. Frequency of the subordinate tactics under different conditions.

ative proportion of multiple foundress colonies should increase. This is exactly what our model predicts: in situations where constraints are low, few individuals choose to be subordinate, and in situations where constraints are high, more individuals choose to be subordinate (Fig. 6).

Survivorship: predation pressure on foraging animals (solitary and subordinate wasps)

When constraints on solitary foundresses are driven by low scale predation pressures (e.g., spider predation), one would expect that these same pressures are inflicted on animals who perform the majority of the foraging events, that is, both solitary and subordinate wasps. When the survivorship of both solitary and subordinate foundresses was increased (Table 1; Altered Scenario 2), the expected percentage of the population choosing to become a subordinate foundress was seen to decrease (Table 3). While increases in survivorship (*see* Reeve 1991) did increase the absolute payoff for subordinate foundresses, their increased survival also increased the absolute payoff for their associated dominant foundress. This difference occurred to such an extent that the effect on the relative payoff of the subordinate decreased. Therefore, from the perspective of relative benefit among individuals, in the case of higher survivorship among subordinates, they had a lower level of success as compared to the expected payoffs achieved by other tactics.

Changing relatedness between collaborators

By altering the degree of relatedness between collaborators on multiple foundress nests (Table 1; Altered Scenario 3), we can examine the relative change in the frequency of multiply founded nests in populations where collaborators are unrelated (baseline scenario) or are related by 0.75 (i.e., when they are full sisters). In most examined populations, we see a range of relatednesses between collaborators, often spanning from 0 to 0.75 (*see* Queller *et al.* 2000, Reeve *et al.* 2000, Liebert & Starks 2006). In a recent review, Nonacs and colleagues (2006) indicated that reproductive skew models are good at explaining group formation when collaborators are related, but not when they are unrelated. Our analysis is in agreement with this, when relatedness is high our model predicts a much higher frequency of individuals willing to be subordinate foundresses (Fig. 6).

Changing degree of reproductive skew between collaborators

Our baseline scenario allows only 20% of the nests reproduction to result from subordinate egg laying. While this degree of skew is not uncommon (*see* Liebert & Starks 2006), the degree of skew can be highly variable from nest to nest. Our model predicts that, as skew between cooperators decreases, we should see an increasing frequency of cooperation. This is also in general agreement with skew models: as the reproductive inducement to collaborate increases, so increases the rate of cooperation.

The model as presented is a good fit with the known biology, and includes all tactics expressed. As such, unlike reproductive skew models, which may suggest when cooperation should exist (*see* Nonacs *et al.* 2006), our model predicts conditions under which all behavioral alternatives are expressed. Ours is a holistic model, which can be extended to any *Polistes* population.

Discussion

Major implications

We have tried to formulate this model in the broadest sense, and in doing so, the predictions from our model provide a framework in which to understand all aspects of *Polistes* nesting biology. Our model is in agreement with observed behavior and existing models of founding tactics and reproductive skew. In interpreting these results, it is imperative to recall that for an individual player within this game theoretic framework,

Table 3. Expected frequencies of alternative tactics. Scenarios are those described in Table 1.

	Baseline (%)	Scenario 1 (High%/Low%)	Scenario 2 (High%/Low%)	Scenario 3 (%)	Scenario 4 (High%/Low%)
Early					
Opportunist	2.7	2.2/3.2	2.1/2.4	1.8	1.8/2.7
Dominant foundress	48.9	41.4/59.7	39.3/43.6	39.8	38.7/42.7
Subordinate foundress	12.2	10.3/14.9	14.7/5.5	33.5	34.6/18.3
Solitary foundress	36.3	46.1/22.2	43.8/48.6	24.9	24.9/36.3
Mid					
Opportunist	4.5	3.8/5.5	3.7/3.9	3.4	3.4/4.6
Dominant foundress	51.8	43.7/63.5	42.5/45.0	47.2	46.2/46.7
Subordinate foundress	6.9	5.8/8.4	8.5/3.0	21.1	21.9/10.6
Solitary foundress	36.9	46.7/22.6	45.4/48.1	28.3	28.5/38.0
Late					
Opportunist	2.1	1.7/2.6	1.7/1.8	1.8	1.8/2.2
Dominant foundress	57.3	47.9/71.2	47.6/48.2	59.0	58.3/53.6
Subordinate foundress	1.5	1.3/1.9	1.9/0.6	5.3	5.5/2.4
Solitary foundress	39.1	49.1/24.3	48.8/49.4	33.9	34.4/41.8

the expression of a particular behavior is based on her own estimation of her condition relative to the rest of the population. Only this way, can individuals be expected to choose tactics resulting in relatively lower payoffs; we would predict this if her expectation, based on her condition, would be a lack of reproductive success via a more profitable tactic.

Our model has generated, for each scenario examined, a relative expected frequency for the occurrence of the founding tactics within the population based upon the expected associated reproductive payoff of each. By examining these relative payoffs under different scenarios (e.g. survivorship, relatedness, etc.) we are able to predict how shifts in constraints should impact the frequencies of the behaviors. By viewing the behaviors according to relative (rather than absolute) expected payoff, it becomes apparent that potentially biologically counterintuitive behavioral shifts can occur (*see* Results).

One of the implicit constraints in our game theoretic model is that the functions of survivorship and average relatedness among individuals remain constant within a given scenario. Relieving these constraints by incorporating a periodic or continuous ability to re-evaluate environmental or individual conditions could lead to profoundly different model outcomes, but these possibilities are not examined here.

It is important to note that we present model derived predicted values as opposed to empirically observed frequencies, and that the relative frequencies of the alternative phenotypes predicted by our model is a good match with the natural setting. In particular, the change in frequency of adopters and usurpers seems to converge with biologically driven predictions. This suggests that the model may reflect reality, and thus may be suitable for modification to adjust to changing conditions.

Although the model is silent on this, it might be reasonable to speculate that the subordinate and usurper tactics are the same. A simple rule may explain the difference in their expression. Upon identifying a nest, an individual will usurp the nest when unrelated to the current foundress and/or powerful enough to depose her. In cases where individuals are related to the current foundress and are not powerful enough to depose

her, the interloper may instead choose to join as a subordinate. In this scenario, no wasp starts out to be a dominant, but rather receives an elevated payoff when a subordinate joins. This perspective fits well within our general framework, where we assume that all tactics are available to all individuals and could explain some of the previously puzzling aspects relating to the existence of subordinate foundresses in unrelated collaborative pairs.

Discriminating between models

We can envision a rough mechanism to determine which model may best describe any given population. The framework can best be viewed as a series of questions. There will be a lot of variation around these questions, but a rule of thumb approach may work reasonably well. Can animals perform more than one tactic? If the answer to this question is no, the system has a high likelihood of best being described by an alternative strategy model, that is, a genetic polymorphism. If the answer is yes, one can ask: Do all animals of a given condition perform only one tactic? If the answer is yes, the system has a high likelihood of best being described by a conditional strategy model. Common conditions may be age, size, and/or experience. If the answer is no, one can ask: Is the relative proportion of animals performing given tactics consistent across time? If the answer is yes, the system may be best described by a mixed strategy model. Our model describes the situation where classes of animals perform tactics in a frequency dependent manner.

Behavioral syndromes

The recent study of behavioral syndromes may provide significant insight into the performance of alternative behaviors (Sih *et al.* 2004a, 2004b). Behavioral syndromes are suites of correlated behaviors that are expressed across contexts. The classic example is aggression, where some individuals are more aggressive and others more passive, which presents to an observer as the performance of different traits (Sih *et*

al. 2004a, 2004b). Sih *et al*. (2004a, 2004b) argue that a behavioral syndrome approach to behavioral research may shed light on seemingly inappropriate behavioral responses (e.g. being too aggressive in a care-giving context such as parental care). This approach can be viewed as a strong alternative to an optimality approach, where an animal is assumed to possess complete behavioral plasticity. A behavioral syndrome approach may be useful here is in understanding how an animal 'chooses' to perform a given tactic, whereas the alternative phenotypes framework described above explains how selection will maintain the alternatives in a population. As such, these approaches can loosely be viewed as complementary in the same general manner as proximate and ultimate approaches to behavior are complementary.

Conclusions

Our current model is sufficient to explain the maintenance of all known alternative phenotypes available to wasps prior to worker emergence. While this paper has tailored the application of this game theoretic understanding to the particular system of nest founding in *P. dominulus*, the same model framework can be applied to any system in which multiple tactics are hypothesized to be dependent on frequency and individual conditions.

Although we only altered single conditions, this model — in its current form — can be used to vary multiple factors simultaneously. In more advanced applications, for example, this model can be modified in such a way as to allow for the incorporation of "error in self-assessment".

The benefits of models are many, but perhaps most satisfying to field biologists is when they generate counterintuitive or novel predictions. For example, our results for predation on both solitary and subordinate foundresses is counter to our general prediction of constraints on solitary founding. This prediction now waits to be tested. Examining the model output also directly led to our speculation that subordinate and usurper tactics are essentially the same, but the expression of either is based on the encountered foundress' relatedness and condition. In

the literature to date, there has been a dearth of comprehensive models whose goal is to provide a unifying framework across all hypothesized systems explaining the maintenance of alternative tactics in a population. By focusing on this greater level of abstraction, such endeavors can then be focused on particular questions (as we have done).

Acknowledgements

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