BALANCING FORAGING AND ANTIPREDATOR DEMANDS: AN ADVANTAGE OF SOCIALITY

Animals foraging in nature must often balance simultaneously feeding and antipredator demands. Predation hazard usually reduces foraging efficiency because foragers may remain sheltered rather than feed, choose less profitable but safer foraging sites, or watch for predators instead of searching for food (Milinski and Heller 1978; Sih 1980, 1992; Werner et al. 1983; Lawrence 1985; Gilliam 1990; Lima and Dill 1990).

Social organization can significantly enhance foraging efficiency under predation hazard because group foragers can often reduce vigilance and increase feeding time compared with solitary foragers (Caraco 1979; Pulliam and Caraco 1984; Cassini 1991; Burger and Gochfeld 1992). Unlike some birds and mammals, the workers of most social bees and wasps do not forage in groups and are thus not able to gain this advantage. But the fact that the workers of social hymenopterans deliver their food recoveries to the colony and do not participate directly in reproduction suggests another possible advantage of sociality.

Our study was stimulated by field observations suggesting more vigilant behavior by solitary than by social bees. A simple explanation for this difference in behavior might be that the death of a social bee forager has minimal effect on overall colony fitness (eusociality results in the decoupling of provisioning and parental care), whereas the death of a solitary bee terminates her fitness entirely. We now believe this explanation to be incorrect: the death of a social bee forager reduces colony reproduction through the loss of her future food recoveries; however, all her past recoveries do add to colony fitness. In contrast, the current day's recoveries of a solitary bee are lost if she is killed before an egg is deposited and the egg-food cell is sealed (Michener 1974; Batra 1984). This difference may account for the observed differences in behavior between social and solitary bees. We constructed models of social and solitary bee foraging behavior under risk of predation, in order to examine this idea.

THE MODELS

In order to model the foraging behavior of social and solitary bees, we first make the simplifying assumption that the number of possible foraging trips per lifetime is unlimited. Biologically this implies a constant probability of mortality (Type II survival rate: R. Dukas and P. K. Visscher, unpublished data) and no senescence. In this case the optimal foraging behavior is identical for all foraging trips, and we can readily derive an analytic solution.

In a second model the total number of possible foraging trips per lifetime was assumed finite. We assumed that bees can employ a flexible foraging strategy, modifying their foraging behavior during their life span. We used dynamic programming to deduce the optimal foraging decision for each trip. The second model yielded similar predictions to those of the first model; for the sake of brevity, we omit further details of the second model.

Social Bee

In our model the social bee makes repeated foraging trips to and from the colony. On each trip the bee chooses a foraging mode M_i. Modes are characterized by two parameters: μ_i, the risk of predation per trip, and ϕ_i, the average food uptake per trip. For simplicity we suppose that these values do not change over time. We do not specify exactly what distinguishes different modes of foraging; examples would be different patches, different degrees of vigilance, or different flight patterns. In practice the number of possibilities might result in virtually a continuum of foraging modes M, but for simplicity we consider only a finite number.

Assuming that the number of possible trips is unlimited, the optimal foraging mode will be the same for all trips. For mode M_i the total expected lifetime food recovery is given by

$$(1 - \mu_i)\phi_i + (1 - \mu_i)^2\phi_i + \cdots = \frac{1 - \mu_i}{\mu_i}\phi_i \tag{1}$$

(by the formula $1 + x + x^2 + \cdots = 1/[1-x]$ for the sum of a geometric series). Maximum lifetime fitness F is obtained by maximizing this expression:

$$F = \max \frac{1 - \mu_i}{\mu_i}\phi_i. \tag{2}$$

If $\mu_i \ll 1$ (predation risk per trip is small), the expression in equation (1) can be approximated by the simpler expression ϕ_i/μ_i. Maximization of this value is equivalent to minimization of its reciprocal:

$$\min \frac{\mu_i}{\phi_i} \quad (\text{if } \mu_i \ll 1). \tag{3}$$

Equation (3) has appealing intuitive content, since the ratio μ_i/ϕ_i represents mortality risk per unit of food recovered. It is related to the "μ/g" rule for ontogenetic habitat switching, derived by Werner and Gilliam (1984). It should be emphasized, however, that equation (3) holds only under a number of quite restrictive assumptions, including absence of growth, senescence, or other effects of age. (See Clark 1994 for further discussion of this model.)

A numerical illustration (using hypothetical data) is given in table 1. Four modes M_i are listed in order of increasing predation risk μ_i and increasing productivity ϕ_i. The optimal mode in this example is M_2, and the expected lifetime of bees employing this mode is $1/\mu_2 = 50$ trips. Notice, however, that modes M_3 and M_4 have greater single-trip expected uptake than does M_2. If the total number

TABLE 1

NUMERICAL EXAMPLE ILLUSTRATING THE OPTIMAL FORAGING STRATEGY
FOR A SOCIAL BEE

Foraging Mode, M_i	Predation Risk per Trip, μ_i	Food Uptake per Trip, ϕ_i	Expected Single-Trip Uptake, $(1 - \mu_i)\phi_i$	Expected Lifetime Uptake, $(1 - \mu_i)\phi_i/\mu_i$
1	.01	1	.99	99
2	.02	3	2.94	147
3	.04	5	4.80	120
4	.10	10	9.00	90

NOTE.—For a single foraging trip, mode M_4 is optimal; for an unlimited number of trips, mode M_2 is optimal.

of possible trips is finite and small, it is intuitively understandable that one of these more productive modes could become optimal. Our second model (not detailed here) showed that this was indeed the case and that bees using the optimal foraging strategy would switch to progressively more dangerous and productive foraging modes as they approached the terminal trip (end of the foraging season).

Solitary Bee

Our model for solitary bees differs from the social bee model in accounting for the fact that food gathered by a solitary bee does not contribute to her reproductive output until an egg is deposited and the egg-food cell is sealed. We assume that egg deposition occurs at the end of each day. A day's foraging involves N trips; reproductive output at the end of each day is assumed proportional to the total food collected by the end of trip N on this day (provided that the bee survives).

The solitary bee has the same choice of foraging modes as the social bee; μ_i and ϕ_i have the same meaning as before. If the bee uses mode M_i and survives the day, her total food accumulation for the day is $N\phi_i$. (In principle, she could switch modes during the day; we will ignore this possibility here but consider it briefly later.) Her expected reproduction per day is therefore equal to

$$(1 - \mu_i)^N \cdot N\phi_i.$$

Total expected lifetime reproduction is thus

$$N\phi_i(\sigma_i^N + \sigma_i^{2N} + \cdots) = \frac{\sigma_i^N}{1 - \sigma_i^N} N\phi_i, \tag{4}$$

where

$$\sigma_i = 1 - \mu_i. \tag{5}$$

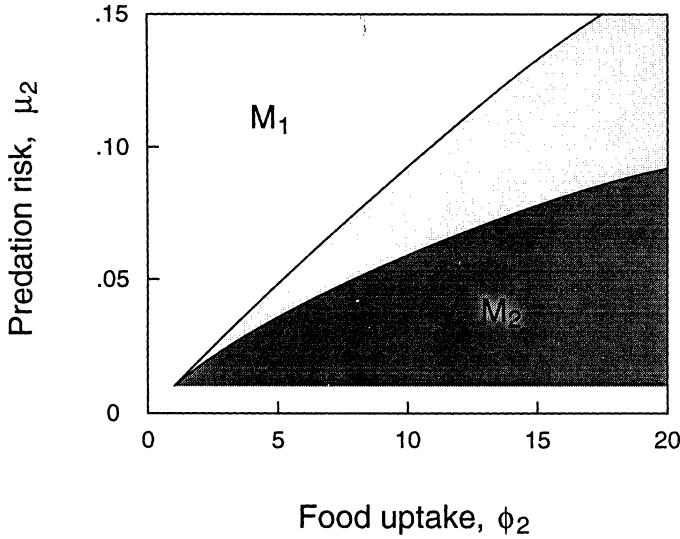The optimal foraging mode (under the present assumptions) is that which maximizes equation (4).

FIG. 1.—Optimal foraging modes for social vs. solitary bees (unlimited number of trips), with a choice of two foraging modes: M_1 ($\mu_1 = 0.01$, $\phi_1 = 1$ unit) and M_2 ($\phi_2 > 0.01$, $\phi_2 > 1$ unit). For points (ϕ_2, μ_2) lying in the *heavily shaded region* labeled M_2, both types of bee should use the more productive, more dangerous mode M_2, while for points in the *unshaded region* M_1, both should use mode M_1. In the *intervening region* the social bee should use M_2 and the solitary bee M_1.

Comparing the optimal strategies for social and solitary bees, in the case that time is unlimited (and the bee does not switch modes during the day), we have

$$\text{social bee: max} \frac{\sigma_i}{1 - \sigma_i} \phi_i \tag{6}$$

and

$$\text{solitary bee: max} \frac{\sigma_i^N}{1 - \sigma_i^N} N\phi_i. \tag{7}$$

The social bee thus optimizes her lifetime reproductive success by considering the mortality-foraging trade-off in terms of single-trip mortality risk, whereas the solitary bee considers the same trade-off in terms of whole-day mortality risk. Inasmuch as the whole-day mortality risk is greater than that for a single trip, we expect solitary bees to use safer but less profitable foraging modes than social bees.

Figure 1 shows this result parametrically, for the case of two foraging modes M_i. The first mode, M_1, is fixed, with $\mu_1 = 0.01$ per trip and $\phi_1 = 1$ unit per trip. The values μ_2 and ϕ_2 are treated as parameters with $\mu_2 > \mu_1$, $\phi_2 > \phi_1$. We assumed $N = 15$ trips per day. Thus, the average life span of a bee using mode M_1 is 6.6 d.

Both types of bee employ the safer mode M_1 if the predation risk μ_2 is high

relative to the benefit ϕ_2 for mode M_2. Also, both types should employ the more dangerous mode M_2 if the benefit ϕ_2 is sufficiently high. However, the solitary bee requires much greater benefits than the social bee, before making this switch, particularly if M_2 is much more dangerous than M_1.

The dynamic programming version of our model (mentioned above) allowed us to consider the possibility that the solitary bee should switch foraging modes during the day. Intuitively, it might seem that she should switch to a safer mode late in the day, in order to safeguard the food already deposited. In fact, what should be safeguarded is her reproductive value (Clark 1994), that is, the sum of expected current reproduction and expected future reproduction. Since the latter is a major proportion of the total, the size of the current deposit may have little effect on optimal foraging behavior. Numerical computation supported this insight; in most cases the optimal strategy did not involve switching modes throughout the day.

DISCUSSION

A solitary bee gains no reproductive fitness from a day's foraging unless she survives to lay an egg and seal it away. On the other hand, a social bee's food recoveries contribute to colony fitness incrementally for each trip, even if she dies during the day. The model presented here indicates that this difference can lead to greater foraging efficiency for the social bee. In other words, optimal balance between foraging and antipredation behavior for workers of social bees provides higher average rates of food uptake in relation to solitary bees. This enhanced foraging performance is probably another advantage of sociality in hymenopterans.

Gadagkar (1990) made a similar argument for the advantage of cooperation in eusocial wasps. He suggested that a worker has an advantage over a solitary foundress because the worker can gain some measure of fitness even if she dies before the completion of food provisioning for larvae. This result occurs because other workers can continue such food provisioning. Our models, therefore, are an explicit application of Gadagkar's "assured fitness return" to the problem of optimal balance between foraging and antipredator demands. Note that, although we discuss here another apparent advantage of sociality, the overall trade-off between solitary and social living is beyond the scope of this note. Aspects of this trade-off have been discussed by Wilson (1971), Michener (1974), Schaffer et al. (1979), Anderson (1984), and Wenzel and Pickering (1991).

In our model, we assumed that bees can choose foraging modes having certain values for rate of food uptake and predation risk. It is well documented that bees can assess the quality and quantity of floral rewards and change their behavior accordingly (see, e.g., Menzel et al. 1974; Heinrich 1979). However, it is still unclear how effectively bees estimate predation risk or respond to it. Morse (1986) found that honey bee and bumble bee foragers exhibit no predator avoidance behavior with respect to crab spiders (Thomisidae), bees' commonest predators at flowers. Both the choice of inflorescences and foraging patterns on inflorescences were identical in the presence and absence of spiders. Bees are even

less likely to detect birds than spiders prior to attack because of the limited resolution of the bees' compound eyes (Land 1981; Dukas and Real 1993). It seems, therefore, that the best antipredator strategies available to bees are either attempting to escape while being attacked or avoiding attack by using devious or erratic flight patterns during foraging. By *erratic flight* we mean flight paths that take indirect routes between flowers or plants and that change direction unpredictably. Erratic flight patterns, well documented for various hymenopterans, are known to reduce the probability of contacts with parasitic flies (McCorquodale 1986; Evans and O'Neill 1988). Erratic flight might be employed as either a constant behavioral strategy or a response to perceived threats such as a failed attack or another indication of heightened predator activity. Note that both erratic flights and false-alarm escape involve costs and therefore reduce foraging efficiency.

The prediction of our models may be tested by examining the response of solitary and social bees (or wasps) to a nearby threat (Morse 1986; Cartar and Dill 1991). Solitary bees should initiate escape more often or from a farther distance from a "predator" than workers of social bees. Alternatively, solitary bees should consistently use more erratic flight patterns than social bees of closely related species. A rigorous test of the model should provide sufficient controls for potential differences in perception and metabolic rate between the species tested. Nevertheless, such differences may reflect only proximate explanations for the ultimate mechanism suggested here.

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