

# Density-Dependent Parasitism and the Evolution of Aggregated Nesting in the Solitary Hymenoptera

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**ABSTRACT** Aggregated nesting is widespread among the solitary Hymenoptera and may represent an important step toward the evolution of eusociality via the semisocial pathway. Five hypotheses have been proposed to explain the evolution of nesting aggregations: first, aggregation may occur in response to a restricted distribution of some key resource; second, aggregation may increase foraging efficiency; third, aggregation may confer improved protection from natural enemies; fourth, aggregation may decrease the cost of nest site search; and fifth, aggregation may increase opportunities to reuse old nests. Proximate explanations for the formation of nesting aggregations, including the philopatry hypothesis, do not compete with these ultimate explanations but, rather, complement them. The role of parasite pressure in favoring or disfavoring aggregated nesting has become an area of active research and debate. This paper reviews field studies of density-dependent foraging by nest parasites and resulting patterns of nest exploitation to test generalizations concerning the effects of parasites. Nest parasites foraged either independently of host nest density ( $n = 2$ ) or they concentrated in areas of high nest density ( $n = 4$ ). Nest parasitism was directly density dependent ( $n = 8$ ), density independent ( $n = 4$ ), or inversely density dependent ( $n = 2$ ). Thus, parasite pressure may favor either aggregated or dispersed nesting. Diversity in patterns of density dependence appears to result from the interaction of variable parasite foraging strategies and host defensive strategies. Inversely density-dependent parasitism may result from parasites being limited by egg supply or handling time, or from improved defense capabilities of grouped hosts. Improved defense may be a product of increased parasite confusion, active group defense, selfish herding, or improved parasite detection. Data supporting these hypotheses are critically reviewed and further research needs are identified.

**KEY WORDS** Insecta, habitat selection, parasites, Hymenoptera

A STRONGLY CLUMPED spatial distribution of nests is a conspicuous feature of the biology of many solitary bees and wasps (Evans 1966a, Michener 1974, Brockmann & Dawkins 1979). Hymenoptera exhibiting aggregated nesting have been studied as model systems for investigations of biotic and abiotic influences on habitat selection (Rubink 1978, Brockmann 1979, Endo 1980, Larsson 1985, Rosenheim 1988). Aggregated nesting also has received attention as a potentially important step toward eusociality; i.e., aggregated nesting facilitates interactions between nesting females, including communal nest sharing, and as such represents an initial step toward eusociality via the semisocial pathway (Lin & Michener 1972, Itô 1980). What factors have favored the evolution and maintenance of nesting aggregations?

## Evolution of Aggregated Nesting

**Five Hypotheses.** Theoretical considerations suggest that aggregated nesting in the Hymenop-

tera, like gregarious tendencies in general, must be favored by some factor to counterbalance the costs of increased intraspecific competition and pathogen transmission. Alexander (1974) discussed three general factors that potentially favor gregarious behavior. First, aggregated nesting may be favored by a restricted distribution of some key resource. Requirements for specific nesting substrates have been demonstrated to contribute to aggregation in some species of ground-nesting wasps and bees (Michener et al. 1958, Rubink 1978, Brockmann 1979, Toft 1987, Weaving 1989). The failure to identify resource-based aggregation in other species may be caused in part by the difficulty of measuring the myriad aspects of microhabitat that could provide relevant cues. Substrate limitation appears, however, to be insufficient to explain nesting aggregations in many hymenopteran systems (Michener et al. 1958, Rubink 1978, Batra 1978, Eickwort 1981, Wcislo 1984, Evans et al. 1986). The roles of the spatial distribution of other key resources such as materials for nest construction, nectar for adult nutrition, or nest provisions (including nectar, pollen, or arthropod prey) have not been investigated.

Second, gregarious associations of females could be favored if they promote increased foraging ef-

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iciency. Although improved foraging through grouping has been demonstrated in other animal taxa (Pulliam & Caraco 1984), solitary wasps and bees have thus far been found to forage strictly individually. The "information center" hypothesis, which postulates that individuals in aggregations obtain information about patchily distributed, ephemeral foraging sites by observing successfully foraging neighbors (Brown 1986), however, could be relevant to hymenopteran nesting aggregations. Thus, although this second hypothesis should not be discarded, there are no data suggesting its applicability to solitary wasps or bees.

Third, aggregated nesting may be favored if it confers improved protection from predators or parasites. Applications of this hypothesis to the Hymenoptera have yielded mixed conclusions; some authors support the notion of a refuge from natural enemies in areas of high nest density, i.e., inversely density-dependent mortality (Alcock 1974, Rubink 1978, Endo 1980, Hager & Kurczewski 1985, Willmer 1985, Gamboa et al. 1986, Evans & O'Neill 1988), and others support the reverse pattern of directly density-dependent mortality (Lin 1964; Lin & Michener 1972; Michener 1974; Brockmann 1979, 1984; Rasnitsyn 1980).

Two additional hypotheses have been proposed specifically to explain the evolution of aggregated nesting in the Hymenoptera. First, Eickwort et al. (1977) suggested that aggregation joiners may use the presence of nesting individuals as a cue to locate suitable nesting sites. As stated, this hypothesis considers only the proximate basis for aggregation formation and not the costs or benefits associated with aggregation. Presumably, however, females joining aggregations by responding to the presence of conspecifics thereby may avoid part of the cost of nest site search. This hypothesis is similar to the limited-resource hypothesis discussed above in that it implies spatial variation in nest site suitability. Furthermore, it assumes that there is a significant cost associated with locating a nest site, an idea supported by observations of extensive nest site searching behavior in *Sphex ichneumoneus* (L.) (Brockmann 1979) and *Ammophila azteca* Cameron (unpublished data), which may extend over many hours. Second, Myers & Loveless (1976) hypothesized that the opportunity to reuse recently abandoned nests or old nests constructed during previous generations might favor aggregated nesting. The ability to reuse old nests is, however, more closely linked to philopatry than aggregated nesting per se; nesting aggregations can occur in areas devoid of preexisting nests (e.g., Evans et al. 1986), and conversely, dispersed nesting can occur in areas harboring old nests (e.g., Michener 1974). The extent to which abandoned nests represent valuable resources for other females of the same generation remains to be demonstrated; reports of nest abandonment and subsequent adoption by neighboring individuals in a wide variety of hymenopteran systems (Brockmann & Dawkins 1979) suggest, how-

ever, that benefits accrued from nest adoption may be significant.

Five hypotheses explaining the evolution of aggregated nesting have thus been proposed. The hypotheses are not mutually exclusive; several factors may simultaneously contribute benefits to aggregated nesting. Three of the hypotheses, those suggesting increased efficiency of foraging, nest site location, and nest construction (by adopting a preexisting nest), will have to be tested in two stages, demonstrating both increased task efficiency with grouping and a resulting increase in realized fitness. In contrast, the hypothesis of improved defense against natural enemies can be tested simply by assessing the incidence of nest failure, a measure with direct relevance to fitness. Certain aspects of the restricted resource hypothesis also may be tested directly by assessing nest failure (e.g., that induced by unfavorable abiotic conditions at the nest site), whereas other aspects of the hypothesis will again require testing in two stages.

**Philopatry.** Philopatry, the choice of nest sites in the same area as the natal nest, is a proximate mechanism of nest site selection rather than an ultimate or functional explanation. It is, therefore, outside the purview of this review. Philopatry may be common, however (Brockmann 1979, Pfennig & Reeve 1989), and its relevance to the evolution of aggregated nesting is a source of some misunderstanding. Therefore, I briefly address the role of philopatry in the formation of nesting aggregations.

Philopatry can be shown to lead to the formation of nesting aggregations without invoking any of the five previously described hypotheses to generate differential reproduction in different nesting areas. Consider the following model. Assume that the available habitat for a ground-nesting bee is divided into 10 identical plots. Assume that an initial population of 100 nesting females is uniformly distributed across the 10 plots such that the initial mean number per plot is 10. Assume that females in each plot have an equal expectation of reproduction but that stochastic factors, present to varying degrees in all systems, contribute variance to progeny production such that 25% of all females produce zero female offspring, 50% produce one female offspring, and 25% produce two female offspring. Assume further that all female offspring choose nest sites within their natal plot (i.e., perfect philopatry). Now, let us follow this population over successive generations, monitoring the variance-to-mean ratio of population size across plots. The variance-to-mean ratio characterizes the bee distribution; a value of 0 indicates a uniform distribution, values between 0 and 1 indicate semiregular distributions, a value of 1 indicates a random distribution, and values >1 indicate clumped, or aggregated, distributions. Philopatry coupled with variance in reproductive rates results in increasing divergence among plot populations with little change in the mean plot population size; thus the

variance-to-mean ratio (the degree of nest aggregation) increases (Fig. 1). Although this process can be independent of any of the five hypotheses for the evolution of aggregated nesting, any factor modulating reproductive rates in different nesting areas will accelerate the formation of aggregations under philopatry. Thus philopatry may be an important proximate basis for aggregation formation.

This line of reasoning leads to the question of the ultimate or functional explanation for philopatric nest site selection. Philopatry may simply evolve because it is energetically expedient; why fly to another nest site if the current location is equally suitable? The physical dimensions of aggregation sites are, however, often so small compared with the range of trivial movements of most Hymenoptera (e.g., to and from feeding, hunting, mating, or sleeping sites) that such an explanation is not very compelling. More intuitive are the suggestions that philopatry may evolve as a means of avoiding the risk of failing to locate another suitable nest site, as a means of avoiding the cost of long-distance movement necessary to locate another suitable nest site, or as a result of any combination of various factors that could make nesting in a previously tested, successful site more advantageous than nesting in an untested nest site. These suggestions, however, have returned us to a consideration of the same factors discussed above as explanations for the evolution of nesting aggregations. For example, a risk of not finding another suitable nest site cannot occur without spatial variation in key resources (hypothesis 1). Philopatry and other proximate explanations are therefore complementary to, rather than competitive with, ultimate explanations for the evolution of nesting aggregations.

### Spatial Density Dependence of Parasite Action

Below, I review empirical studies of density-dependent foraging by nest parasites and the resulting patterns of nest parasitism in the solitary Hymenoptera to test generalizations regarding the importance of parasite pressure in favoring aggregated nesting. Foraging is measured as a time commitment through direct observations of parasite behavior, whereas nest parasitism is assessed by examining nest contents. No attempt is made to distinguish between active, behaviorally mediated parasite aggregation (in which parasites choose to forage in areas of higher host density) and passive, demographically mediated aggregation (in which parasite populations build up over several generations in areas with abundant host resources) (Rosenheim et al. 1989). What is crucial here is not the mechanism by which a parasite distribution is generated but rather the form of the final distribution. Hypotheses of parasite physiological and behavioral limitations and host defensive strategies are investigated as explanations for observed pat-

terns of inversely density-dependent nest parasitism. Areas requiring additional experimental work are identified.

To what extent is one pattern of density-dependent nest parasitism generalizable within the solitary Hymenoptera? Field studies of interspecific, spatially density-dependent parasitism (Table 1) revealed examples of each of the three possible outcomes: direct density dependence ( $n = 8$ ), density independence ( $n = 3$ ), and inverse density dependence ( $n = 2$ ). The only study of intraspecific nest parasitism, involving theft of provisions or egg replacement, suggested a pattern of density independence. These diverse results were observed despite the fact that parasites foraged either independently of host density ( $n = 2$ ) or concentrated in areas of high host density ( $n = 4$ ); in common with insect parasitoids in general, inversely density-dependent foraging has not been documented (Lessells 1985, Rosenheim et al. 1989). Wcislo (1984) has carefully described a system in which a strong pattern of inversely density-dependent parasitism was produced despite directly density-dependent parasite foraging. Patterns of inversely density-dependent parasitism are of special interest because they provide an explanation for the evolution and maintenance of nesting aggregations. How can we explain the diversity of spatial patterns of parasitism in general, and inversely density-dependent parasitism in particular?

**Parasite Limitations.** The first class of explanations centers on behavioral and physiological limitations of the foraging parasites. In a process analogous to predator satiation in areas of high prey density, parasites encountering high concentrations of host nests may be constrained by the availability of either mature oocytes (or uterine larvae in the case of sarcophagid parasites), or handling time required to parasitize each nest successfully (Hassell 1982, Lessells 1985). Stochastic variation in parasite foraging behavior also may translate directly density-dependent foraging into inversely density-dependent parasitism (Morrison 1986).

Some confusion exists regarding the effect of parasite limitations on the relationship between patterns of foraging and patterns of nest parasitism. Specifically, is it valid to suggest that an increasing ratio of foraging parasites to hosts is required to generate directly density-dependent parasitism (Wcislo 1984, Larsson 1986)? Empirical and theoretical studies of parasite-host interactions suggest that the answer is no, and that weaker forms of aggregation also will produce directly density-dependent parasitism (Hassell 1978, 1982). This may be understood by considering the parasite's functional response, which describes the relationship between host density and the number of hosts attacked per parasite per unit time. Functional response curves are generally approximately linear with positive slopes over low host densities, gradually approaching zero slope at higher host densities (Hassell 1978). If we first assume a linear

functional response and no egg limitation, theory predicts that a random distribution of parasites will result in density-independent parasitism and that any degree of aggregation in areas of high host density will result in directly density-dependent parasitism. It is only if we assume instead that the parasite shows the most extreme form of egg limitation (i.e., each parasite can deposit only one egg) that we obtain a requirement for an increasing parasite-to-host ratio to generate directly density-dependent parasitism. Parasites in nature will not be completely free of behavioral and physiological limitations, nor will they show this most extreme form of limitation. The minimal strength of parasite aggregation required to generate directly density-dependent parasitism will therefore fall somewhere between that defined by a random distribution of parasites and a constant parasite-to-host ratio. This conclusion may, however, need to be modified if hosts have effective defensive strategies, as discussed below. In addition, any host defensive measure that increases the parasite's host handling time, including false burrows (e.g., Evans 1966b), empty cells (e.g., Tepedino et al. 1979), or difficult-to-penetrate nest closures (Trexler 1985), will increase the strength of the aggregation necessary to generate directly density-dependent parasitism. One factor that may constrain the ability of parasites to aggregate is territorial interactions between parasites, as observed in *Nomada* spp. (Rozen et al. 1978, Cane 1983).

Unfortunately, data with which to assess hypotheses of parasite limitations are scant. The parasitic fly *Metopia campestris* (Fallén) did not appear to be limited by the availability of larvae to deposit; 25 sampled flies carried a mean of 31.6 uterine larvae (range, 7–61) (Weislo 1986). Neither were the more fecund chrysidid wasps dissected by Iwata (1964) likely to be constrained in this way. Iwata (1964) does, however, describe a number of chrysidids with exceptionally small inventories of mature oocytes, including five species with  $\leq 3$  oocytes. In addition, Alexander & Rozen (1987), in a review of ovary condition in 39 parasitic bee species, found a mean of only 7.18 mature oocytes per individual (range, 2–21), despite an observed trend toward increased numbers of ovarioles and mature oocytes compared with nonparasitic bee lineages. It is difficult, however, to infer the likelihood of egg limitation from comparative studies of mean oocyte number. What is needed are more intensive studies of individual species relating oocyte inventory to foraging behavior. Studies also are needed to address potential constraints imposed by host handling time. This additional work will be required to assess critically the significance of parasite behavioral and physiological limitations. Theory does suggest, however, that these limitations will be increasingly likely to play a role under conditions of increasingly high host density.

**Nest Defense.** The second class of explanations for inversely density-dependent parasitism centers

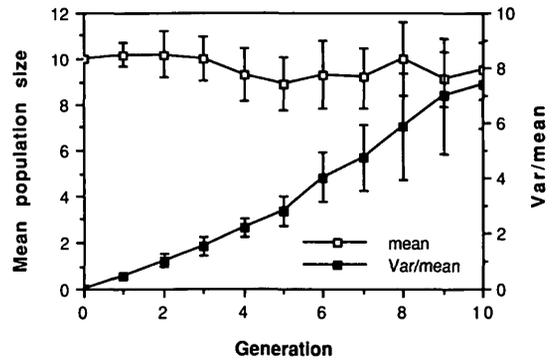


Fig. 1. Influence of philopatric nest site selection and stochastic variation in individual reproduction on the formation of nesting aggregations. Plotted are the mean plot population size and the variance-to-mean ratio (both  $\pm$ SE, calculated from four simulation replicates) versus number of generations since the initial uniform distribution.

on improved defense capabilities of grouped hosts (Bertram 1978, Pulliam & Caraco 1984). I discuss the relevance of four hypotheses of improved defense to the solitary nest-building Hymenoptera: predator (or parasite) confusion, active group defense, selfish herding, and improved parasite detection.

**Predator Confusion.** The predator confusion hypothesis suggests that prey capture by visual predators may be made more difficult when prey form tight groups, thereby preventing the predator from focusing on an individual prey target. Although developed primarily for schooling fish or herding mammals (Bertram 1978), abundant circumstantial evidence suggests that this hypothesis may be applicable to many Hymenoptera. Visual tracking of wasps and bees returning to nests with provisions is the primary tactic for host location of many nest parasites, including primarily sarcophagids (Newcomer 1930; Ristich 1956; Alcock 1974, 1975; Hager & Kurczewski 1985; Itino 1986; McCorquodale 1986; Spofford et al. 1986; Rosenheim 1987a) but also an anthomyiid (Batra 1965), a bombyliid (Rosenheim 1987a), and a chrysidid (Tsuneki 1968). The importance of this visual tracking is dramatically reflected in the evolutionary incorporation of complex evasive behavior into the nest-approach flights of many wasps and bees (Batra 1965; Alcock 1974, 1975; Hager & Kurczewski 1985; McCorquodale 1986; Spofford et al. 1986; Evans & O'Neill 1988).

Some wasps respond to the detection of parasites with modified or amplified evasive maneuvers (Alcock 1974, 1975; Hager & Kurczewski 1985; McCorquodale 1986; Spofford et al. 1986). Many wasps also incorporate motionless periods, or "freezes," into their nest-approach flights (Alcock 1974, 1975; Evans 1970; Peckham 1985; Hager & Kurczewski 1985; McCorquodale 1986; Spofford et al. 1986; Evans & O'Neill 1988) or while they are

active at nests (Rosenheim 1988). Freeze-stops appear to be effective because parasites respond to host movement. A parasite's attention may be diverted from a motionless host by the movement of neighboring individuals, resulting in the escape of the initially tracked individual (Alcock 1974, Evans 1970, Peckham 1985, Hager & Kurczewski 1985, McCorquodale 1986). Similar distraction may occur at other stages of evasive flights (Hager & Kurczewski 1985). Note that this does not simply imply a short- or long-term shifting of the burden of parasitism among individuals (i.e., selfish herding), because parasites may be diverted to conspecific males or to females not engaged in a vulnerable stage of the nesting cycle (e.g., Miller & Kurczewski 1973). Parasites also may be distracted by other host-tracking conspecifics (Endo 1980, Itino 1988), an effect that might become more important within nesting aggregations if parasites show directly density-dependent foraging.

Of the systems reviewed in Table 1, two involve parasites that visually track their hosts. Contrary to the expectations of the predator confusion hypothesis, *Amobia floridensis* (Townsend) generated directly density-dependent parasitism (Freeman & Taffe 1974). The interaction of *Amobia distorta* Allen with its two eumenid hosts (reported in Itino [1988] and reanalyzed here in the appendix) appears, however, to support the predator confusion hypothesis. Strong directly density-dependent parasite foraging consistently produced density-independent parasitism (Itino 1988, current study), a result hypothesized by Itino (1988) to be attributable to mutual interference between host-tracking parasites. General considerations of other systems involving visual parasites have additionally led to predictions of inversely density-dependent parasitism (Alcock 1974, Hager & Kurczewski 1985). Quantitative studies testing these predictions are needed to assess further the potential role of parasite confusion in generating inversely density-dependent parasitism. Specifically, we need to explain the relationship between local nest density and the density of foraging parasites, the probability that a host returning to a nest will be detected by a parasite, and the probability that visual tracking will be disrupted by the presence of conspecific hosts.

**Active Group Defense.** Active group defense of aggregated nests is conspicuous in some ground-nesting Hymenoptera. Observations have revealed simultaneous attack by several host bees on a single intruding parasite (Thorp 1969), as well as the defense of neighboring nests by individual bees (Batra 1978, Thorp 1969) and wasps (Genise 1979). In addition, high densities of males searching for mates in nest aggregations could interfere with effective parasite foraging (Miller & Kurczewski 1973). The significance of these forms of group defense remains undocumented, however, despite the suggestion by Wcislo (1984) that interference from host wasps, other parasites, and other passing in-

sects might play an important role in modifying the effect of a parasitic fly. It also is not known if territorial males guarding their mates' nests from parasites (e.g., Hook & Matthews 1980, Brockmann & Grafen 1989) might incidentally defend adjacent nests, resulting in improved protection of nests in aggregations.

**Selfish Herding.** One form of improved defense potentially available to individuals in a nesting aggregation is taking cover from natural enemies behind neighboring individuals. Hamilton (1971) developed this "selfish herd" hypothesis to explain the centripetal instincts of animals faced with predators approaching from a peripheral position; it may be applicable to studies of within-aggregation patterns of nest parasitism (e.g., Wcislo 1984; Table 1), but not to studies of between-aggregation patterns of parasitism conducted on a larger spatial scale (e.g., Freeman 1982; Table 1). Although Wcislo (1984) and Larsson (1986) have interpreted nesting aggregations as selfish herds, neither their studies nor any other reviewed in Table 1 has suggested a peripheral approach for nest parasites, which instead seem to be most abundant in areas of highest nest density. Apterous natural enemies, and especially apterous predators which do not emerge from host nests in the midst of aggregations, may be likely to exhibit peripheral approach. Predatory ants, important natural enemies of the solitary nest-building Hymenoptera (e.g., Larsson 1986, Rosenheim in press), may be particularly important.

Host species that enforce parasite exclusion from central areas of nesting aggregations through individual or group defense might profitably be investigated for selfish herding effects. At present, however, there are no data to suggest that aggregation of nests is the cumulative result of many selfish acts; in systems showing inversely density-dependent parasitism, aggregation may instead be mutualistic. Nest density, rather than geometric position relative to the center of the aggregation, appears to be the critical factor.

**Parasite Detection.** The final means by which grouping may improve nest defense is through improved detection of approaching parasites. Improved detection, although potentially relevant to those Hymenoptera with effective defenses, has not yet been demonstrated in any hymenopteran system. Indeed, the significance of host vigilance and parasite detection in general is only beginning to be explored (e.g., Hager & Kurczewski 1986; Spofford et al. 1986; Rosenheim 1987a, 1988).

In summary, no single spatial pattern of density-dependent nest parasitism appears to be broadly applicable to the Hymenoptera. Thus, parasitism pressures may favor either aggregated or dispersed nesting or have little influence on the costs and benefits of aggregated nesting. Variation in patterns of density dependence appears to be generated by the interplay of different parasite foraging strategies and different defensive strategies of hosts.

**Table 1.** Review of field studies of spatial density dependence of parasite foraging and nest parasitism in the solitary Hymenoptera

Host species (family)	Parasite species (family)	Size of study area	Para- site for- aging <sup>a</sup>	Para- sites orient to host or nest	No. host gener- ations per analysis	Parasit- ism <sup>b</sup>	Reference
Interspecific parasitism							
<i>Hoplitis anthocopoides</i> (Schenck) (Megachilidae)	A complex, primarily <i>Monodontomerus montivagus</i> Ashmead (Torymidae)	Albany Co., N.Y. (about 1,300 km <sup>2</sup> )	—	Nest	1	DDD	Eickwort 1973 <sup>c</sup>
	<i>Anthrax irroratus irroratus</i> Say (Bombyliidae)		—	Nest			
<i>Sceliphron assimile</i> Dahlbom (Sphecidae)	<i>Melittobia</i> sp. (Eulophidae)	Island of Jamaica (about 11,400 km <sup>2</sup> )	—	Nest	≥20	DDD	Freeman & Parnell 1973, Freeman 1977
<i>Sceliphron assimile</i> Dahlbom (Sphecidae)	<i>Melittobia</i> sp. (Eulophidae)	18–28 m <sup>2</sup>	—	Nest	≥35	DDD	Freeman & Ittyeig 1976
<i>Sceliphron asiaticum</i> (L.) (Sphecidae)	<i>Melittobia</i> sp. (Eulophidae)	Island of Trinidad (about 4,800 km <sup>2</sup> )	—	Nest	≥30	DDD	Freeman 1982
<i>Sceliphron fistularium</i> (Dahlbom) (Sphecidae)	<i>Melittobia</i> sp. (Eulophidae)	Island of Trinidad (about 4,800 km <sup>2</sup> )	—	Nest	≥30	DDD	Freeman 1982
A complex <i>Sceliphron caementarium</i> (Drury) (Sphecidae)	<i>Trichrysis tridens</i> (Lepeletier) (Chrysididae)	Several km <sup>2</sup>	DI <sup>d</sup>	—	1	—	Trexler 1984
<i>Trypargilum politum</i> (Say) (Sphecidae)						—	
<i>Chalybion californicum</i> (Saussure) (Sphecidae)						—	
<i>Trypoxylon palliditarse</i> Saussure (Sphecidae)	A complex, primarily <i>Photocryptus</i> sp. (Ichneumonidae)	Island of Trinidad (about 4,800 km <sup>2</sup> )	—	—	Many	IDD <sup>e</sup>	Freeman 1981
	<i>Brachymeria mexicana</i> (Dalla Torre) (Chalcididae)		—	—			
	<i>Melittobia</i> sp. (Eulophidae)		—	Nest			
	undetermined (Sarcophagidae)		—	—			
<i>Trypargilum politum</i> (Say) (Sphecidae)	<i>Melittobia</i> sp. C (Eulophidae)	—	—	Nest	1	DI	Trexler 1985 <sup>f</sup>
<i>Crabro cribrellifer</i> (Packard) (Sphecidae)	<i>Metopia campestris</i> (Fallén) (Sarcophagidae)	130 m <sup>2</sup>	DDD	Nest	1	IDD	Wcislo 1984, 1986
<i>Bembix rostrata</i> L. (Sphecidae)	<i>Metopia leucocephala</i> (Rossi) (Sarcophagidae)	1,000 m <sup>2</sup>	DDD	Nest	1	—	Larsson 1986 <sup>g</sup>
<i>Ammophila dysmica</i> Menke (Sphecidae)	<i>Argochrysis armilla</i> Bohart (Chrysididae)	250 m <sup>2</sup>	DDD	Nest	1	DI	Rosenheim 1987b, 1989
<i>Ammophila dysmica</i> Menke (Sphecidae)	<i>Argochrysis armilla</i> Bohart (Chrysididae)	0.125 km <sup>2</sup>	—	Nest	1	DDD	Rosenheim 1987b, 1989
<i>Episyron arrogans</i> (Smith) (Pompilidae)	<i>Metopia sauteri</i> (Townsend) (Sarcophagidae)	About 0.044 km <sup>2</sup>	DI	Nest <sup>h</sup>	1	—	Endo 1980
<i>Eumenes colona</i> Saussure (Eumenidae)	<i>Melittobia</i> sp. (Eulophidae)	Island of Jamaica (about 11,400 km <sup>2</sup> )	—	Nest	≥20	DDD	Freeman & Taffe 1974
	<i>Amobia floridensis</i> (Townsend) (Sarcophagidae)		—	Host		DDD	
<i>Pachodynerus nasidens</i> (Latreille) (Eumenidae)	<i>Melittobia</i> sp. (Eulophidae)	Island of Jamaica (about 11,400 km <sup>2</sup> )	—	Nest	Many	DDD	Freeman & Jayasingh 1975
Two hosts <i>Anterhynchium flavomarginatum</i> Smith (Eumenidae)	<i>Amobia distorta</i> Allen (Sarcophagidae)	About 2 km <sup>2</sup>	DDD	Host	1	DI	Itino 1986, 1988; current study <sup>f</sup>
<i>Orancistrocerus drewseni</i> Saussure (Eumenidae)						DI	
Intraspecific parasitism							
<i>Ammophila subulosa</i> L. (Sphecidae)	<i>Ammophila sabulosa</i> L. (Sphecidae)	190–360 m <sup>2</sup>	—	Nest	1	DI	Field 1987

<sup>a</sup> DDD, directly density dependent; DI, density independent.

<sup>b</sup> DDD, directly density dependent; DI, density independent; IDD, inversely density dependent.

<sup>c</sup> Nest density measured qualitatively ("aggregated" versus "scattered" nests).

<sup>d</sup> No significant declines in two parasite populations isolated from others by >0.8 km were observed following experimental removal of most of the host populations.

Spatial patterns of parasitism also may be sensitive to changes in mean host density (Hassell 1982) or to the spatial scale at which pattern is analyzed (Walde & Murdoch 1988, Rosenheim et al. 1989).

Additional work is needed to determine which hypotheses of parasite limitations and host defenses explain inversely density-dependent parasitism. Additional work also is required to understand the proximate basis for gregarious nesting. What is the relative importance of first, passive formation of aggregations through spatially varying reproductive rates coupled with philopatric nest site selection, and second, active habitat selection? If active habitat selection is important, do females respond primarily to the presence of conspecifics or associated cues, or do females respond independently to other indicators of suitable nest sites? A more complete understanding of the proximate basis for nest site selection decisions should contribute significantly to investigations of the evolution of aggregated nesting.

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<sup>c</sup> Data in Table 1 of Freeman (1981) were reanalyzed to assess density dependence of parasitism (Spearman's rank correlation,  $r_s = -0.482$ ,  $df = 23$ ,  $P < 0.05$ ).

<sup>f</sup> Study conducted with artificially constructed nest aggregations.

<sup>g</sup> Larsson (1986) discusses other potential nest parasites and predators; however their relationship to *B. rostrata* is unknown.

<sup>h</sup> Endo (1980) suggests that *M. sauteri* may also show some attraction to the host.

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### Appendix

Itino (1988) reported one of the few studies of parasite foraging and nest parasitism that was replicated over different host generations and years. His analysis is, however, flawed in that it combined data from different years and, unlike several studies cited in Table 1 (e.g., Freeman 1977, 1982), included sites that were sampled in different years. Thus, spatial density dependence was confounded with potential temporal effects.

Therefore, I have reanalyzed the original data (T. Itino, personal communication). Each host generation is analyzed separately. Each experimental shed (which housed a number of artificial trap nests) is treated as a single data point. Spatial density dependence of nest parasitism was assessed by performing a linear regression of percentage of parasitism (dependent variable) on *F*, an index of host density (independent variable; see Itino [1988]), with each point weighted by the number of host cells dissected to estimate percentage of parasitism (Table A1). Spatially density-dependent foraging by the parasite *A. distorta* was assessed by performing a linear regression of mean number of parasites counted during 5-min censuses (dependent variable) on the number of eumenid hosts nesting per shed, with each point weighted by the number of censuses performed (Table A2).

The reanalysis confirms Itino's (1988) conclusion of directly density-dependent foraging by *A. distorta* (Table A1), but contrary to Itino (1988), it finds no support for directly density-dependent nest parasitism (Table A2). The failure to reveal directly density-dependent parasitism does not appear to be a result of the smaller sample sizes produced by analyzing each host generation individually; host generations with the largest sample sizes (e.g., 1981 and 1983 generations of *A. flavomarginatum*) yielded the strongest evidence of density independence.

**Table A1. Reanalysis of Itino's (1988) data on spatially density-dependent foraging by the parasite *A. distorta***

Yr and host generation	No. sheds censused	Total no. censuses performed	<i>r</i>	<i>P</i>	<i>B</i> ± SE
1982, 2	8	95	0.577	0.1345	0.0238 ± 0.0138
1983, 1	24	106	0.618	0.0013	0.0402 ± 0.0109
2	19	83	0.730	0.0004	0.0380 ± 0.0086
1984, 1	10	39	0.649	0.0423	0.0535 ± 0.0222
2	16	66	0.492	0.0531	0.0269 ± 0.0127

**Table A2.** Reanalysis of Itino's (1988) data on spatially density-dependent nest parasitism of *A. flavomarginatum* and *O. drewseni* by the parasite *A. distorta*

Yr and host generation	Total no. cells sampled	Total no. cells parasitized	Mean % parasitism	No. sheds sampled	<i>r</i>	<i>P</i> <sup>a</sup>	<i>B</i> ± SE
<i>O. drewseni</i>							
1980, 2	115	25	21.7	5	0.342	0.574	-0.0080 ± 0.0127
1981, 2	45	10	22.2	10	0.423	0.223	-0.0295 ± 0.0223
1982, 2	82	1	1.2	8	0.772	0.043	0.0043 ± 0.0017
1983, 1	87	2	2.3	19	0.120	0.626	0.0011 ± 0.0023
2	84	14	16.7	7	0.372	0.411	0.0143 ± 0.0160
1984, 2	55	8	14.5	6	0.801	0.056	0.0184 ± 0.0069
<i>A. flavomarginatum</i>							
1980	22	3	13.6	4	0.993	0.008	0.0436 ± 0.0038
1981	233	72	30.9	16	0.003	0.992	0.0002 ± 0.0211
1982	43	9	20.9	7	0.533	0.218	0.0212 ± 0.0150
1983	154	22	14.3	21	0.321	0.156	0.0119 ± 0.0080

<sup>a</sup> To maintain the experiment-wide  $\alpha = 0.05$ , the critical *P* value for the 10 regressions is 0.005.