

a significantly nonrandom distribution (Table 1). A greater than expected number of workers were observed grooming once ('nonspecialists') and several times ('specialists'), with fewer than expected observed an intermediate number of times. In Colony 2, black and cordovan nestmates observed grooming did not differ significantly in their propensity to specialize ($P > 0.10$, Mann-Whitney U test). Specialists did not differ significantly in age-class from non-specialists in either colony ($P > 0.50$, G -test); they comprised only 5.29% (Colony 1) and 5.96% (Colony 2) of all groomers, but engaged in 31.65% (Colony 1) and 29.05% (Colony 2) of all grooming bouts. In marked contrast, individual workers did not specialize on feeding nestmates (Table 1).

Social insect workers often specialize on tasks that appear to require the learning of particular skills for efficient performance^{3,4}. The coupling of patrilineal differences in the propensity to groom with individual specialization suggests a corollary to the proposal^{29,30} that the genetically heterogeneous worker population produced by a multiply mated queen may constitute a selective advantage to colonies in variable environments. Specifically, a colony's ability to cope with unpredictable events that require the reaction of a varying number of experienced workers (as may the response to ectoparasites by grooming specialists) may be enhanced by genetic variation in the threshold at which workers first respond to appropriate stimuli. Moreover, multiple mating by queens need not be a strategy to select for particular genotypes; genetic variation in initial response threshold rather than specific thresholds *per se* may suffice.

Determining what role behavioural genetic variation plays in colony social organization will ultimately require an assessment of the array of tasks for which it is maintained, the set of ecological³² and social^{33,34} contexts in which it is expressed, and the effect of such variation on patriline and colony fitness.

Since submitting this manuscript, we have learned that Robinson and Page³⁵ report similar results.

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Clutch size adjustment by a swallowtail butterfly

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Because life-history characters such as breeding schedule, reproductive investment, and age-specific survivorship exhibit great variation in nature and are closely linked to individual fitness, the development of a theory of life-history evolution is a major focus of evolutionary biologists¹⁻³. One life-history trait that has received much attention is clutch size, the number of eggs laid by a female during a round of reproduction. For parasitic organisms such as herbivorous insects and parasitoids, two models have been developed which describe the evolution of behaviour influencing clutch size^{4,5}. These models both make two predictions: (1) that individuals should adjust clutch size so that larger clutches are laid on hosts that can support the growth of more offspring, and (2) that as time between oviposition bouts increases, as would occur when hosts become rarer, larger clutches should be laid on hosts of a given quality. We present here the first empirical test of these predictions and show that the pipevine swallowtail butterfly, *Battus philenor*, adjusts its clutch size in response to variation in both host quality and time since last oviposition.

We performed an experiment in the field to determine whether females modify clutch size in response to variation in host-plant characters and lay larger clutches on plants of higher quality. If characteristics of the host plant, *Aristolochia reticulata* (Aristolochiaceae), do not influence clutch size, there should be no correlation between clutch size and any plant characters. But clutch size was significantly correlated with most plant characters we measured, suggesting that females modify clutch size depending on the characteristics of the plant (Table 1). Because young plants have fewer, smaller leaves and longer, wider buds than old plants and *A. reticulata* leaves become sclerophyllous and less edible as they age⁶, the observed correlations suggest that females lay larger clutches on younger plants with more edible foliage.

This conclusion is supported by examination of the size at which test larvae disperse from host plants. We removed original clutches from plants and then seven days later (normal egg

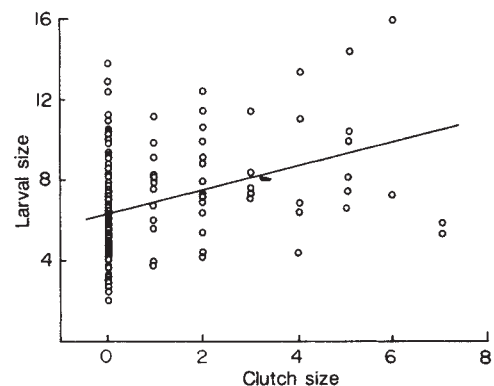


Fig. 1 Correlation between egg cluster size and mean length at dispersal of test larvae on each plant ($r = 0.33$, $P < 0.0001$, $n = 163$). Laboratory data show that both plant quality and time since last oviposition affect clutch size. In the field experiment time since last oviposition was not controlled and this is probably one reason for scatter in the data presented here. For methods see Table 1.

Table 1 Correlations between plant and butterfly characters.

Plant character	Clutch size	Mean length of test larvae
Bud length	$r = 0.15$	$r = 0.36$
	$P < 0.06$	$P < 0.0001$
	$n = 162$	$n = 162$
Bud width	$r = 0.29$	$r = 0.53$
	$P < 0.009$	$P < 0.0001$
	$n = 79$	$n = 79$
Number of leaves	$r = -0.27$	$r = -0.29$
	$P < 0.0005$	$P < 0.0002$
	$n = 162$	$n = 162$
Leaf area	$r = -0.28$	$r = -0.15$
	$P < 0.0002$	$P < 0.06$
	$n = 163$	$n = 163$

Correlations between plant characters, clutch size, and mean length of two test larvae at dispersal. (r = correlation coefficient; P = probability level; n = sample size, number of clutches.) During March and early April 1980 at the John Henry Kirby State Forest in Tyler County, Texas, USA, we followed females searching for their host plant, *Aristolochia reticulata* (Aristolochiaceae). This species has determinant growth and only produces new foliage during a short period in the early spring. As the foliage matures it becomes sclerophyllous and a poor substrate for larval growth. A single plant rarely contains enough young foliage to support the complete growth and development of a larva. Consequently, when larvae have consumed all edible foliage on a plant, they disperse to new ones. The probability that a larva will survive to discover a new host plant is proportional to its size at dispersal⁷. For each host plant on which a female alighted we recorded the number of eggs laid, removed any eggs laid, and measured terminal bud length, bud width, number of leaves, and total leaf area⁸. Seven days later, the normal duration of egg development in the field, we placed two randomly chosen newly hatched test larvae on each host plant. We censused the plants daily and recorded the length of each remaining larva and the data and cause of disappearance of each missing larva⁹. Larval length and mass are highly correlated⁷. We used only plants on which both larvae disappeared by dispersal because for these plants the mean size of the two test larvae should reflect the amount of edible foliage on the plant.

development time) placed two randomly chosen newly hatched larvae on the plants. Mean size at dispersal of the two test larvae increased with increasing cluster size (Fig. 1), indicating that females tend to place larger clusters on plants with more edible foliage, supporting prediction (1) above. As expected, larval size at dispersal, like egg cluster size, is negatively correlated with plant size, and positively correlated with bud size (Table 1).

We performed a second experiment in the laboratory to test both predictions under more controlled conditions than was possible in the field. Our rationale was to control both the quality of a host plant on which a female was allowed to lay eggs and also the readiness of a female to do so, which is expected to increase with time since the last oviposition. All females tested progressed through three distinct levels of discrimination (see legend to Table 2). Females rejected all plants, regardless of food quality, immediately after laying eggs. After this initial rejection period, females accepted high-quality plants but rejected those of low quality. Finally, after this discrimination phase, females accepted both types of plant. Females thus consistently discriminate between high- and low-quality *A. reticulata* plants in a way very similar to the way butterflies discriminate among different host species⁹.

Females at the same discrimination level presumably represent those with a similar readiness to lay eggs. By comparing the mean clutch size of such females on hosts of different quality, we tested whether host quality affects clutch size independently of readiness to lay eggs. Such an effect exists for *B. philenor*: for females that have just accepted both the high- and low-quality plants, mean clutch size is significantly larger on high-quality plants than on low-quality plants (Table 2). This parallels

our field results, indicating that females tend to lay larger clutches on plants with young, edible foliage, and supports prediction (1).

By allowing females with different discrimination levels to lay eggs on plants of the same quality, the effect on clutch size of a female's readiness to lay eggs can be assessed independently of host quality. Females that have just accepted both high- and low-quality plants lay larger clutches on high-quality plants than females that have only accepted high-quality plants (Table 2). This result implies that the longer a female goes without laying eggs on a host plant, the larger her clutch size will be when she does so, supporting prediction (2).

Insects discriminate between different host plant species when deciding to lay eggs¹⁰⁻¹⁸ and a female's discrimination level may progress through well defined stages⁹. Our results indicate that this kind of progression also characterizes discrimination between individual plants within a host species. In *B. philenor* host-plant selection involves first locating an individual of an appropriate host and then, depending on the quality of the plant and the discrimination level of the female, determining a clutch size ranging from zero to some maximum. Our results suggest that there is some physiological variable that increases with time since last oviposition but decreases with each egg laid. One commonly suggested candidate for a physiological variable with these properties is egg load¹⁹, which could be monitored by stretch receptors in the abdomen.

Table 2 Average egg cluster size in each treatment.

Quality of plant	Discrimination level	
	Accept high quality plant only (1)	Accept both plants (2)
High	2.73 (0.43)	7.27 (1.14) ($P < 0.006$)
Low		3.20 (0.46)

P -values indicate significance level of difference between treatments (Mann-Whitney U -test; $n = 15$ for all treatments). Numbers in parentheses are standard errors. In the summer of 1985 in our laboratory in Durham, North Carolina, USA, mated females were allowed to lay eggs on a high-quality *A. reticulata* plant until they refused to accept that plant for oviposition. This procedure reduced all females to the same low level of readiness to lay eggs. Before testing, each female was randomly assigned to one of three treatments. In treatment 'high-1', females were permitted to lay eggs on a high-quality plant as soon as they accepted the high-quality plant but before they accepted the low-quality plant. In treatment 'high-2', females were permitted to lay eggs on the high-quality plant as soon as they accepted both the high- and low-quality plants. Finally, females in treatment 'low-2' were allowed to lay eggs on the low-quality plant as soon as they accepted both the high- and low-quality plants. Plant appearance changes dramatically with age. High-quality plants had six young tender light green leaves and two large terminal buds. Low-quality plants had six old sclerophyllous darker green leaves and no terminal buds. Forty-seven females were used in this experiment. All 47 accepted the high-quality plant before accepting the low-quality plant. Of these 47, 15 had been assigned to treatment high-1 and were allowed to lay eggs immediately. Of the remaining 32, 30 later accepted the low-quality plant and then were allowed to lay eggs on either the low-quality plant (treatment low-2) or the high-quality plant (treatment high-2). The remaining two females never accepted the low quality plant and were removed from the experiment. Following the methods of Singer⁹, after a female's readiness had been zeroed, females were placed alternately on a high- and low-quality *A. reticulata* plant every 4-5 minutes. A female was considered to have accepted a plant on which she was placed if she curled her abdomen to the foliage in an attempt to lay eggs, since this behaviour is almost invariably followed by oviposition. If continued testing of the female was desired, she was removed from the plant before any eggs were laid. A female was considered to have rejected a plant if she either assumed a basking position or flew off the plant.

Most theoretical and empirical investigations of the evolution of clutch size have considered organisms with parental care that lay one clutch per season²⁰⁻²². By contrast, many short-lived organisms such as insects lay several clutches within a season and then die. Although in these organisms the variation in clutch size is large, both between species and among individuals^{10,23-26}, theory developed for seasonal breeders is of little help in

accounting for this variation. Two recent models, however, specifically address this type of variation in herbivorous and parasitic insects^{4,5}. Our results substantiate two of the predictions of these models, suggesting that their underlying assumptions are valid for at least one species of herbivore.

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Early vision and texture perception

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Texture perception has frequently been studied using textures constructed by repeated placement of micropatterns or texture elements. Theories have been developed to explain the discriminability of such textures in terms of specific features within the micropatterns themselves. For example, Beck^{1,2} observed that a region filled with vertical Ts is readily distinguished from one filled with tilted Ts but not from one filled with vertical Ls. He attributed this to the different distribution of oriented line segments present in the former case but not in the latter. However, Bergen and Julesz³ found that a region of randomly oriented Xs segregated from one filled with randomly oriented Ls, in spite of the identical

distribution of oriented line segments in the two cases. They suggested that this discrimination might be based on the density of such features as terminators, corners, and intersections within the patterns. We note here that simpler, lower-level mechanisms tuned for size may be sufficient to explain this discrimination. We tested this by varying the relative sizes of the Xs and the Ls; when they produce equal responses in size-tuned mechanisms they are hard to discriminate, and when they produce different size-tuned responses they are easy to discriminate.

Figure 1a shows an example of a texture composed of Xs within a texture composed of Ls, similar to the texture used by Bergen and Julesz. The X and L micropatterns are each made of two perpendicular bars, and the bars making the Xs have the same length and thickness as the bars making the Ls. The textures are easily distinguished, and Bergen and Julesz suggested that discrimination could be accomplished by mechanisms that measured the differing densities of micropattern features; for example the Xs have four terminators each, while the Ls only have two; the Ls have a corner while the Xs do not; and so on. This type of description was motivated by analysis of many textures constructed of small micropatterns made up of line segments, dots or other discrete components.

Fig. 1 Top row, Textures consisting of Xs within a texture composed of Ls. The micropatterns are placed at random orientations on a randomly perturbed lattice. *a*, The bars of the Xs have the same length as the bars of the Ls. *b*, The bars of the Ls have been lengthened by 25%, and the intensity adjusted for the same mean luminance. Discriminability is enhanced. *c*, The bars of the Ls have been shortened by 25%, and the intensity adjusted for the same mean luminance. Discriminability is impaired. Bottom row, The responses of a size-tuned mechanism. *d*, response to image *a*; *e*, response to image *b*; *f*, response to image *c*.

