consisting of nine blocks of 48 trials. The nine blocks were devoted to each of the nine combinations of the three different tilt conditions and three different amounts of displacement of the middle point (2, 4, or 6 percent of the 3-D distance between the two endpoints). Three sessions were devoted to displays with perspective projections and three to displays with parallel projections.

Detection accuracy was a linear function of the magnitude of the 3-D displacement of the middle point and was unaffected by variation in the 3-D tilt or by perspective projection (Fig. 2A). (Performance was virtually identical for all three observers, so only the average data are plotted in this and subsequent graphs.) A single linear function accounted for 98.3 percent of the variance in accuracy among the 18 conditions. Therefore, the geometric information for this discrimination must have been some aspect of the 3-D structure that remained invariant under projective transformations.

The best measure of the magnitude of displacement in this task is the percentage of the distance between the two endpoints rather than the absolute angular distance at the retina. This derives partly from the geometrical fact that this percentage remains invariant under motion in 3-D space and partly from empirical evidence, not reported here, that detection of a given percentage displacement remains invariant under scalar changes in distances among the three points.

In experiment 2 we compared the performance of this distance acuity task with that of more familiar vernier acuity tasks. Whereas the distance acuity task involved collinear displacements that altered only the distances among the points, the vernier acuity task involved orthogonal offsets that altered the collinearity of the points. These patterns were presented only in the 2-D projective plane.

Accuracy was slightly higher in the vernier acuity task in eight of the nine conditions, although the overall difference was not statistically significant by analysis of variance. Both tasks were similarly affected by the distance between the endpoints, depending on the relative percentage rather than the absolute retinal distance of the displacement. Additional experiments have shown, however, that acuity in both of these 2-D tasks is lower than with displays of three stationary points, presumably owing to the rotary motion of the present displays.

In a final experimental test of the 3-D structure of the visual information we asked observers to detect displacements from the 2-D center (rather than the 3-D center) of patterns whose endpoints were rigidly rotated in 3-D space and displayed by perspective projection onto the *xy* display screen. Three observers served for two sessions, one of which was devoted to detection of centers in 2-D space and the other to the detection of centers in 3-D space. The 3-D tilt—0°, 30°, 45°, or 60°—was randomly varied between trials. One block of 96 trials in each session was devoted to the detection of one of two different amounts of displacement—2 or 3 percent. Observers were not significantly better than chance at detecting the 2-D centers of these patterns (Fig. 2C). The reason for the difficulty of the 2-D task was that the displays still appeared as 3-D, but the middle point appeared neither centered nor rigidly connected to the endpoints.

We have also found that motion is necessary for the perception of 3-D distance in these displays. When observers were presented with stationary patterns like that in Fig. 1C, they detected the 3-D centers little better than chance, though few errors occurred when the same set of points was sequentially displayed as three points rotating in 3-D space.

The general finding is that precise visual measures of 3-D structure can be derived from the invariant structure of optical patterns undergoing perspective transformations.

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References and Notes

1. E. Ludvigh, *Am. J. Ophthalmol.* **36**, 139 (1953); L. Riggs, in *Vision and Visual Perception*, C. Graham, Ed. (Wiley, New York, 1965); G. Westheimer, *Invest. Ophthalmol. Visual Sci.* **18**, 893 (1979).
2. D. G. Burr and J. Ross, *Vision Res.* **19**, 523 (1979); G. Westheimer and S. P. McKee, *J. Opt. Soc. Am.* **68**, 450 (1978); *ibid.* **70**, 772 (1980).
3. J. E. Cutting and L. T. Kozlowski, *Bull. Psychon. Sci.* **9**, 353 (1977); G. Johansson, *Psychol. Res.* **38**, 379 (1976); *Sci. Am.* **232**, 76 (June 1975); J. S. Lappin, J. F. Doner, B. L. Kottas, *Science* **209**, 717 (1979); S. Ullman, *The Interpretation of Visual Motion* (MIT Press, Cambridge, Mass., 1979).
4. L. Matin, in *Handbook of Sensory Physiology*, vol. 7, part 4, *Visual Psychophysics*, D. Jameson and L. M. Hurvich, Eds. (Springer-Verlag, Berlin, 1972).
5. R. Fox and R. Patterson *Percept. Psychophys.* **30**, 513 (1981); B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971); J. S. Lappin and L. D. Preble, *Percept. Psychophys.* **17**, 439 (1975); W. R. Uttal, J. Fitzgerald, T. E. Eskin, *Vision Res.* **15**, 939 (1975).
6. G. Johansson, in *Stability and Constancy in Visual Perception*, W. Epstein, Ed. (Wiley, New York, 1977).
7. J. J. Gibson, *The Senses Considered as Perceptual Systems* (Houghton Mifflin, Boston, 1966); J. R. Platt, in *Symposium on Information Theory in Biology*, H. P. Yockey, R. L. Platzmann, H. Quastler, Eds. (Pergamon, New York, 1958); R. Shaw, M. McIntyre, W. Mace, in *Perception: Essays in Honor of James J. Gibson*, R. B. MacLeod and H. L. Pick, Jr., Eds. (Cornell Univ. Press, Ithaca, N.Y., 1975).
8. The measure of accuracy, from Luce's choice theory [R. D. Luce, in *Handbook of Mathematical Psychology*, R. D. Luce, R. R. Bush, E. Galanter, Eds. (Wiley, New York, 1963)], was defined by the equation,
$$-\ln \eta = (1/2) \ln \left\{ \frac{[N(y|C) + 0.5][N(n|D) + 0.5]}{[N(n|C) + 0.5][N(y|D) + 0.5]} \right\}$$
where y and n represent the responses "yes" and "no," C and D represent the two stimulus alternatives, centered and displaced, and $N(\ )$ represents the number of trials on which the designated response was made to the designated stimulus. This measure was used because it corrects for biases in the tendency to respond "yes" or "no" and because it has the mathematical properties of a measure of distance. This measure is similar to the signal detection measure, d'.

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Social Wasps: Discrimination Between Kin and Nonkin Brood

Abstract. *In experiments in which nest boxes were switched, colony foundresses of the social wasp* Polistes fuscatus *accepted sisters' combs with little brood destruction but destroyed younger brood in the combs of less closely related females and sometimes deserted these combs. Discrimination between related and unrelated brood does not appear to depend on prior brood contact or environmentally acquired cues.*

It is well known that adult social insects discriminate between nestmates and other conspecifics, probably using odors (*1, 2*). Despite the importance of adult-brood interactions in the evolution and maintenance of insect sociality, little is known about the frequency or mechanism of adult-brood discrimination (*2*). In particular, the ability of adults to discriminate among brood on the basis of adult-brood relatedness is unexplored, although heritable recognition cues have recently been strongly implicated in adult-adult kin discrimination in several social insect species (*2, 3*). We now report that colony-founding queens of a social wasp, *Polistes fuscatus*, discriminate between brood-filled combs (nests) of their sisters and those of less closely related females, possibly through the use of inherited cues.

In a study conducted at the Macbride Field Campus of the University of Iowa, we used free-living *P. fuscatus* colonies housed in artificial nest boxes. To establish sisterhood among females, we marked young potential queens in mature fall colonies (1980) with colony-specific paint codes. In March 1981, we placed 150 identical nest boxes at intervals of 5 to 30 m along forest-meadow boundaries within a range of 3 km. Most of the boxes were eventually occupied by overwintered colony foundresses that had been marked with individual codes. There was one comb per nest box.

The experimental manipulation consisted of simultaneously chasing two foundresses from their nest boxes and switching the nest boxes. Thus each foundress encountered the comb and nest box of the other female at her nest site upon her return (*4*). Switches were made between foundresses previously marked on the same natal combs (SS, sister switches) and those that were either marked nonsisters or females of unknown parentage (NS, nonsister switches) whose colonies were at least 300 m apart. Females nesting at this distance are not likely to be closely related, because very few marked foundresses in the study started colonies at locations more than 50 m from their natal sites. All experiments were conducted before workers emerged, and with few exceptions (*5*), only colonies with single foundresses were used. Nonsister switches were conducted at three stages of development: eggs only (E stage), eggs and larvae (L stage), and eggs, larvae, and pupae (P stage). Sister switches were made at only E and P stages because single-foundress sister colonies were in short supply (most of the marked sisters joined associations).

The criteria for brood discrimination were destruction of brood or desertion of foreign combs by recipient females within 4 days after the nest box switch. Control experiments showed no evidence that experimental procedures affected a returning female's response to brood (Table 1).

We found that relatedness of females to foundresses of foreign brood markedly affected their treatment of the brood. Brood destruction occurred in 30 of 34 nonsister comb switches as opposed to 6 of 24 sister switches ($P < 0.001$, χ^2 test). Nonsisters ate significantly more eggs and ate or ejected more of the smaller larvae than did sisters across all stages of colony development (Fig. 1 and Table 1). Also, 12 of 34 nonsisters deserted new combs, whereas all 24 sisters adopted theirs ($P < 0.01$, χ^2 test) (*6*). Most brood were destroyed, and most desertions (8 of 12) took place within 1 hour after the females' first contact with foreign combs.

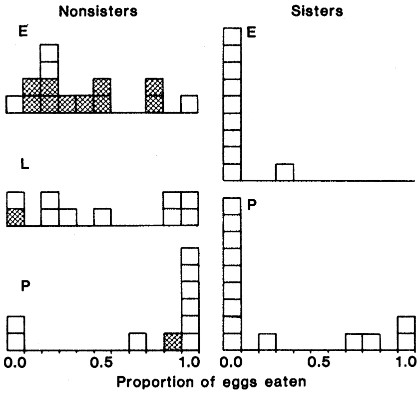

Fig. 1. The proportion of eggs eaten in switched combs as a function of relatedness of recipient foundresses and successive stages of colony development (see text for definition of E, L, and P). The number of eggs available in any comb were 9 to 17 (E stage), 6 to 14 (L stage), and 4 to 18 (P stage). Each square represents a switched comb; hatched squares represent combs deserted by recipient females.

These results indicate that *Polistes* foundresses may use heritable cues in brood discrimination since, to the best of our knowledge, switched females had never encountered each other's nests. However, acceptance of a sister's comb and brood may be due to proximity effects, because most females nested within 15 m of their sisters. Thus, (i) sisters' combs may acquire similar odors through use of similar food or nest material or (ii) females nesting close to each other may habituate to each other's combs through intervisitation. (Although such visits by single foundresses were not observed, they could not be ruled out because colonies were not under close surveillance.) To test these hypotheses, we switched two pairs of SS-E combs located over 100 m apart (intervening tree belts increased their isolation) and two pairs of NS-E combs located within 15 m of each other (data included in Table 1). All four sisters accepted their new combs and ate no eggs, whereas the four nonsisters ate eggs and deserted ($P = 0.014$, Fisher's exact test). Therefore, common nesting environment or recent contact probably are not involved in discrimination between a sister's and a nonsister's comb. However, the effects of sisters' common history on the natal comb as opposed to their genetic relatedness on comb acceptance have yet to be tested.

It is uncertain whether a female accepts a sister's comb because she cannot tell the difference between it and her own comb, or if she can discriminate between them but tolerates the sister's brood. Extensive brood destruction in four sister switches (Fig. 1) suggests that at least some females can recognize a sister's comb as being foreign, although the data are inadequate to firmly establish this generalization. Wide variation in response by both sisters and nonsisters (Fig. 1) may reflect a highly polymorphic

Table 1. Brood destruction by foundresses exposed to the comb of either a sister or a nonsister (switches). Control females encountered their own combs. A "natural" control consisted of the removal and subsequent replacement of a female's nest box while she was absent. Females were chased from their nest boxes before nest box removal in "forced departure" controls. In "new box" controls, females were chased from their nest, which was then glued into a new nest box before its replacement. Controls were otherwise treated like experimental colonies (*4*). The proportion of brood destroyed is given in parentheses.

Manipulation	Stage of colony (oldest brood present)	Number of colonies	Number of brood destroyed			
			Eggs	Young larvae (instars 1 to 3)	Mature larvae (instars 4 to 5)	Pupae
			Switches			
Sisters	Eggs	10	3* (.03)			
Nonsisters	Eggs	14	54 (.31)			
Nonsisters	Larvae	10	46 (.43)	6 (.10)	1 (.02)	
Sisters	Pupae	14	41* (.23)	10* (.11)	1 (.01)	2 (.01)
Nonsisters	Pupae	10	94 (.79)	22 (.52)	0	0
			Controls			
Natural	Eggs	6	0			
New box	Eggs	9	0			
Forced departure	Eggs	9	1 (.01)			
Forced departure	Larvae	10	1 (.01)	0	0	
Forced departure	Pupae	10	0	0	0	0

*$P < 0.001$, χ^2 comparisons of sisters and nonsisters. In addition, ten undisturbed colonies were monitored for brood destruction. In these colonies, 2 of 306 eggs, 6 of 301 larvae, and 1 of 176 pupae were eaten across all stages of colony development.

genetic basis of discrimination, which might allow sister-sister discrimination.

The locations of the cues used in discrimination are not known. Egg-stage switches indicated that eggs or the comb, or their combination, are adequate for discrimination of a sister's comb from a nonsister's. For several reasons (*7*) we suspect that discrimination cues reside in the comb, not in brood members themselves, and are odors applied by the foundress (*8*). If foundresses do odor-mark combs, then brood discrimination may be based on the same cues as those used by *Polistes* females in adult kin recognition (*9*).

The reproductive status of preworker brood depends largely on their order of eclosion. Early emergents are workers, whereas later females are more likely to be potential queens (males do not appear until later in the summer). For this reason, age-biased responses to foreign brood could be expected and, in fact, such a bias appeared (Table 1); eggs were more often destroyed than were younger larvae, and older larvae and pupae were seldom destroyed. Also, the proportion of brood destroyed increased in older combs for both nonsister and sister switches (*10*). Desertions were uncommon in later nonsister switches as compared to NS-E switches (Fig. 1); only one NS-L and one NS-P female deserted (neither female was relocated).

Response to foreign brood on the basis of relatedness might be important for *Polistes* females in at least two natural contexts: (i) cooperative colony-founding associations of sisters (*11*) and (ii) usurpation of a single foundress's comb by another female (*12, 13*), usually one of unknown origin (*13*). Subordinate foundresses in associations tolerate their dominant sisters' brood and thereby probably increase their own inclusive fitness. In contrast, usurpers show age-specific brood destruction patterns very similar to those observed in our nonsister experimental switches (*13*). Older brood are spared and are later, as workers, exploited by the usurper to rear her own offspring. By destroying brood the usurper gains three probable advantages: (i) cells are emptied for her own eggs, (ii) she removes a competitor's genes, and (iii) brood eaten by herself or fed to older larvae are a valuable food resource.

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References and Notes

1. E. O. Wilson, *The Insect Societies* (Belknap, Cambridge, Mass., 1971).
2. B. Holldobler and C. D. Michener, in *Evolution of Social Behavior: Hypotheses and Empirical Tests*, J. H. Markl, Ed. (Verlag Chemie, Weinheim, 1980).
3. L. Greenberg, *Science* **206**, 1095 (1979); A. R. Jutsum, T. S. Saunders, J. M. Cherett, *Anim. Behav.* **27**, 839 (1979); M. D. Breed, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 2635 (1981).
4. Nests were matched as closely as possible for comb size, position in the nest box, and brood composition. A 20-minute interval passed between removal and replacement of nest boxes. An empty nest box was placed within 5 to 10 m of each switched nest box. We observed foundresses for an hour after their return and mapped the brood in the combs before switches and after observation. We also mapped brood and counted adults at 2-day intervals in all study colonies from nest initiation until emergence of the first workers or loss of the queen or comb.
5. The exceptions included three SS-P colonies that had two foundresses each and a pair of SS-P colonies, used in SS-E switches, whose queens had been later replaced by sisters. There is no evidence that these substitutions affected the experimental results.
6. Two of the deserting females joined nearby sisters and two started new combs in adjacent empty nest boxes. The other eight were not seen again.
7. Egg-eating tended to follow an all-or-none pattern in switch combs, suggesting that the comb and brood are assessed as a unit; the larvae and pupae of ants and bees are easily transferred between colonies and sometimes between species (*2*). Honey bee workers, however, discriminate between haploid and diploid drone larvae on the basis of site-independent cues [J. Woyte, *J. Apic. Res.* **4**, 65 (1965)].
8. Behaviors that may involve comb-marking include mixing saliva with wood fibers used in comb construction and rubbing the abdominal venter over the comb and its pedicel [G. J. Gamboa and H. E. Dew, *Insectes Soc.* **28**, 13 (1981); D. C. Post and R. L. Jeanne, *J. Kans. Entomol. Soc.* **54**, 599 (1981)].
9. N. Ross and G. J. Gamboa, *Behav. Ecol. Sociobiol.* **9**, 163 (1981); J. Shellman and G. J. Gamboa, *ibid.* **11**, 51 (1982).
10. Comparison of NS-E egg destruction with that in later stages may be inappropriate because some NS-E females deserted new combs before contacting all of the brood in them.
11. L. Pardi, *Physiol. Zool.* **21**, 1 (1948); M. J. West-Eberhard, *Misc. Publ. Mus. Zool. Univ. Mich.* **140**, 1 (1969).
12. G. J. Gamboa, *Science* **199**, 1463 (1978).
13. J. E. Klahn, thesis, University of Iowa (1981).
14. We thank J. Kirchner, C. Larch, D. Pfennig, and H. K. Reeve for field assistance and the University of Iowa for permission to conduct studies at the Macbride Field Campus. We also thank M. L. Winston, G. R. Buckle, L. Greenberg, B. Hölldobler, L. Johnson, S. Hubbell, D. Feener, and J. Howard for reviewing our manuscript. Partial funding was provided by an Oakland University Summer Faculty Fellowship and NSF grant BNS-81-15932 (to G.J.G.).

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Male Firefly Mimicry

In a report of mimicry by male *Photuris* fireflies, Lloyd presents "a complex of behavioral mimicries that is without known parallel in the animal kingdom" (*1*). Lloyd previously suggested that some *Photuris* females are aggressive mimics, mimicking the female flash of a foreign species in order to attract the foreign males as food (*2*). Here, he proposes that *Photuris* males mimic foreign male flash patterns in order to attract *Photuris* females for mating. Although Lloyd's excellent observations could be interpreted as mimicry, other mechanisms may be involved.

Lloyd's interpretation of mimicry is based on a correlational study, the apparent similarity between male *Photuris* flashes and the male courtship flashes of other firefly species. Lloyd noted similarities in flash patterns produced by *Photuris*, *Photinus*, and *Pyractomena* males, but most of his examples include flickers, glows, and single flashes, which are fairly widespread types of luminescence often seen in various firefly species. Such similarities may be incidental.

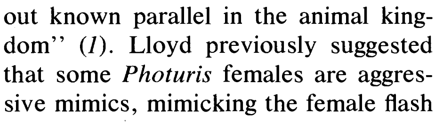

Fig. 1. Twinkles (small peaks) and crescendo flashes (large peaks) from a *Photuris lucicrescens* male during courtship. Scale bar, 2 seconds.

Mimicry by *Photuris* males would seem not to be a reproductive strategy because any male adopting this pattern will be eaten by the predatory aggressive mimic *Photuris* female that responds (something that actually occurs whenever *Photuris* males are placed in a container with *Photuris* females whether or not flashing occurs). Lloyd avoids this difficulty by assuming that male mimicry permits a male to "locate a hunting female with marginal valence for hunting and change her to a mating condition (seduction-mimicry)" (*1, 3*), but he provides no evidence that this happens. Observations on *Photuris versicolor* argue against this hypothesis (*4*). In this species only mated females adopt the behaviors (photic, locomotory, and postural) of the aggressive mimic. Virgin females do not become aggressive mimics. After mating, a behavioral switch to predation takes place. There are, apparently, no reports of aggressive mimics mating with males, and I have never observed aggressive mimics switching back to virgin answering behavior. Hence, a *P. versicolor* male that adopts the reproductive strategy of simulating the mating signal of the male of another species risks destruction, for only a predatory *Photuris* female will be attracted to such signal, not a reproductively active female. The behavioral switch *may* be different in other *Photuris* species (*5*).