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An Analysis of the Interrelationships Among Nest Variables in *Polistes exclamans* (Hymenoptera: Vespidae)

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ABSTRACT: Principal components analysis is performed on 11 variables of *Polistes exclamans* nests, brood and associated adults in nest collections made in June, July and September. Four biologically meaningful principal components were found: (1) nest size, (2) nest growth, (3) nest decline, and (4) nest parasitism. In each sample nest size accounted for most of the variance, followed by nest parasitism. Comparisons among populations using principal components values instead of individual measures make more complete use of available information.

Nest measurements are often central to studies of social wasps (Richards, 1978; Oster and Wilson, 1978). Nests can be compared with respect to the following variables: how many cells the nests contain, the developmental stages of the brood, numbers of new and old cells, species of parasites and numbers of parasitized cells, total numbers of males and females, their approximate age, and the females' ovarian development. Not only may the values of these variables vary but the interrelationships among them may also differ over time or among different types of nests. The present study examines the interrelationships among 5 nest variables and 6 individual wasp variables, using principal components analysis. Principal components analysis is used because it provides an unbiased method of weighting individual variables. A comparison of the differences in biological meaning of significant components in different samples provides a way of looking at changes in the interrelationships among variables from one sample to another. The study population consists of 3 summertime collections of *Polistes exclamans* nests and their associated wasps from San Antonio, Texas.

Methods

Three collections of *P. exclamans* nests and their associated wasps were made in San Antonio, Bexar County, Texas on 20-22 June, 26-28 July and 10 September, all in 1977. All nests were collected using techniques previously described (Strassmann, in prep.). In this species workers and queens

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sometimes form satellite nests near the main nest (Strassmann, in press, in prep.). These satellites must be identified and associated with the proper nest for a full understanding of the population biology of the sample (Strassmann, in prep.). In June and July main nests and their satellite nests were identified and these nests were then distinguished from independent nests lacking satellites (Strassmann, in prep.). All individuals were classified into 3 age categories according to the degree of sclerotization of the frontal edge of the ventral abdominal sclerites: (1) younger than 6 days, (2) 6–15 days, (3) more than 15 days old (West Eberhard, 1975; Strassmann, in press). Ovaries were dissected and for the purposes of this analysis grouped into (1) non egg-layers with partially developed and undeveloped ovaries, (2) intermediate egg-layers with developing oocytes in at least 3 ovarioles but only one fully developed ripe egg, and (3) egg-layers with fully developed ovaries containing several ripe eggs, and developing oocytes in all six ovarioles. Cases of ovarian regression were placed in the first category when regression meant they had no layable eggs in their ovaries. All nests were examined, and total numbers of new cells, pupae, and hatched cells were counted. The two parasitoids found in these samples, *Elasmus polistis* (Hymenoptera: Chalcidoidea: Eulophidae) and *Chalcoela iphitalis* (Lepidoptera: Pyralidae) leave clear and easily distinguishable evidence of their presence in the cells (Rau, 1941; Reed and Vinson, 1979). Numbers of infested cells were counted. While some males were present in June and September, they were absent in July. To facilitate comparisons among the three samples, numbers of males were omitted from all evaluations.

Each nest was thus characterized by the following 11 variables: (1) number of non egg-layers, (2) number of intermediate egg-layers, (3) number of egg-layers, (4) number of females more than 15 days old, (5) number of females 6-15 days old, (6) number of females younger than 6 days old, (7) number of pupae, (8) number of hatched cells, (9) number of new cells, (10) number of *E. polistis*-parasitized cells, and (11) number of C. &Ma&parasitized cells.

Analysis of the factors responsible for variation in nest size and composition is complex because we are considering a set of variables rather than one variable. A logical method for overcoming this difficulty is principal components analysis (Hotelling, 1933; Anderson, 1958). With this method a set of n correlated real variables is replaced by a set of uncorrelated variables, principal components, which are linear transformations of the original variables with weights chosen to maximize the explained variance. The extent to which a single principal component can explain the bulk of the variance depends on the extent to which the original variables are correlated. If the original variables are highly correlated in similar directions, the first principal component may explain most of the variance. A principal component is statistically meaningful if the eigenvalue is greater than one

Table 1. Association of variables with 4 biologically real multivariate patterns.

	Nest size	Nest growth	Nest decline	Nest parasitism
Non egg-layers	X			
Intermediate egg-layers				
Egg-layers		X		
Old wasps	X		X	
Middle aged wasps	X			
Young wasps	X	X		
Pupae	X			
Hatched cells	X		X	
New cells	X	X		
E. polistis				X
C. iphitalis				X

when principal components are computed from a matrix of correlations. A component may be statistically significant and yet still have no clear biological meaning, so in this analysis only those components which were both statistically significant and had clear biological meaning are compared among samples. The components were calculated from a matrix of correlations among the variables to avoid the bias towards the variable with the greatest variance that results if the principal components are computed from raw, unstandardized data (Schull and Neel, 1965). Varimax rotation was used in the present principal component analysis to simplify interpretation of the correlation patterns, and component scores were computed using the Statistical Package for the Social Sciences (Nie et al., 1975).

Results and Discussion

Principal components were calculated for June, July and September, first considering each nest separately, then grouping satellites with the main nest they came from and considering the sum as one large nest, called a satellite system. The principal components were then calculated for (A) independent nests alone, (B) main nests alone, (C) satellite nests alone, (D) satellite systems, and finally (E) satellite systems and independent nests (together called nest systems).

Four biologically meaningful principal components were found: (1) nest size, (2) nest growth, (3) nest decline, and (4) nest parasitism (Table 1). In addition certain logical combinations of the-above occurred. Nest decline was always associated with C. *iphitalis* parasitism. Depending on the sample, nest size was occasionally associated with nest growth or nest decline. Table 1 presents associations between the 11 variables and the 4 biologically meaningful principal components. Statistically significant components not fitting any of these patterns, or reasonable combinations thereof, or not having clear biological meanings separate from the above components were

Table 2. Principal components of nest parameters in 3 collections of nests in San Antonio, Texas with the percent of variation accounted for by each component. a. Each nest or satellite nest treated independently. b. Satellite nests added to their main nests and independent nests.

	All nests, June (N = 75)			All nests, July (N = 41)			All nests, Sept. (N = 32)		
a.	1	2	3	1	2	3	1	2	3
Non egg-layers	.90	−.06	.28	.92	.25	.18	.64	.46	.50
Intermediate egg-layers	−.04	.58	.39	−.08	−.04	−.89	.79	.27	−.17
Egg-layers	.16	−.10	.79	.31	.25	.73	−.10	.63	.08
Old wasps	.49	.10	.67	.32	.70	.19	.76	−.02	.51
Middle-aged wasps	.68	−.02	.21	.86	.08	.17	.78	.46	.27
Young wasps	.85	−.15	−.13	.87	.01	.04	.30	.84	.14
Pupae	.79	.01	.19	.71	.29	.07	−.03	.12	.95
Hatched cells	.85	.14	.08	.45	.82	.15	.65	.52	.40
New cells	.59	.02	.26	.87	.02	.20	.16	.81	−.03
E. polistis	.07	.77	−.07	−.05	.00	.00	.11	.04	.95
C. iphitalis	−.06	.79	−.12	−.09	.95	.09	.83	−.36	−.17
Eigenvalue	4.36	1.64	1.06	5.02	1.80	1.21	5.08	1.96	1.75
% variance explained	39.7	14.9	9.7	45.6	16.4	11.0	46.1	17.8	15.9

	Nest systems, June (N = 55)			Nest systems, July (N = 30)		
b.	1	2	3	1	2	3
Non egg-layers	.96	.03	.15	.96	.18	.09
Intermediate egg-layers	.27	.61	.17	.03	−.06	−.07
Egg-layers	.73	.10	.38	.70	.28	−.02
Old wasps	.78	.26	.27	.54	.62	.43
Middle-aged wasps	.82	−.06	−.03	.88	.05	.03
Young wasps	.79	−.21	.11	.91	.05	−.05
Pupae	.87	.60	.21	.77	.21	−.10
Hatched cells	.88	.14	−.04	.51	.80	.16
New cells	.26	−.03	.90	.94	.01	.00
E. polistis	−.09	.60	.54	−.09	−.05	.97
C. iphitalis	−.10	.83	−.18	−.12	.94	−.23
Eigenvalue	5.39	1.68	1.03	5.54	1.70	1.26
% variance explained	49.0	15.2	9.3	50.4	15.5	11.4

rejected. Principal components of the fourth order or higher generally lacked biological meaning, and therefore are not presented in Tables 2 and 3. Table 4 presents a summary of the biological meaning of the principal components for each collection and each nest type.

In June and July the first principal component is clearly nest size (Table 2a, b), both for nests and for nest systems. In both months all variables except intermediate egg-layers, and the parasitoids *Elasmus polistis* and *Chalcoela iphitalis* loaded positively on the first component which explained 39.7 percent of the variance in June and 45.6 percent of variance in July.

Table 3. Principal components of nest parameters for independent nests, main nests and satellite nests and satellite systems, with the percent of variation accounted for by each component. a. June b. July.

	Independent nests (N = 41)			Main nests (N = 16)			Satellite nests (N = 18)			Satellite systems (N = 13)		
a. June	1	2	3	1	2	3	1	2	3	1	2	3
Non egg-layers	.93	−.20	.08	.88	.35	.04	.78	.54	.12	.91	.38	.09
Intermediate egg-layers	−.06	.64	.59	−.18	−.28	.74	.14	.13	.74	−.08	.08	.93
Egg-layers	.12	−.26	.71	.13	.88	−.04	−.11	−.09	.84	.75	.39	.31
Old wasps	.79	−.12	−.09	.24	.80	.25	.77	.20	.45	.51	.58	.54
Middle-aged wasps	.68	.01	.38	.82	.12	.27	.14	.87	−.07	.88	.02	−.14
Young wasps	.58	−.22	.26	.86	.02	−.31	.63	.27	−.05	.93	−.04	−.24
Pupae	.78	.20	−.08	.84	.23	−.23	.08	−.01	.15	.94	−.18	.27
Hatched cells	.82	.12	.07	.84	.24	−.04	.80	−.20	−.11	.79	.40	−.13
New cells	.60	.07	.41	.82	−.08	−.06	.06	.92	.15	.84	−.19	.19
E. polistis	.14	.78	−.22	.20	.29	.74	.93	−.06	.20	.14	.84	.15
C. iphitalis	−.12	.79	−.06	−.23	.31	.54	.59	.06	.69	−.16	.85	−.02
Eigenvalue	4.16	1.85	1.13	4.90	2.01	1.16	4.38	1.94	1.58	5.85	2.27	1.23
% variance explained	37.9	16.9	10.3	44.5	18.3	10.6	39.8	17.7	14.4	53.2	20.6	11.2

	Independent nests (N = 23)			Main nests (N = 7)			Satellite nests (N = 11)			Satellite systems (N = 7)		
b. July	1	2	3	1	2	3	1	2	3	1	2	3
Non egg-layers	.90	.37	.10	.90	.42	−.02	.41	.48	.75	.99	.06	−.05
Intermediate egg-layers	−.22	−.53	−.07	−.21	−.80	.18	.75	−.07	.15	.43	.84	.04
Egg-layers	.49	.61	−.09	.16	.80	.50	−.37	.71	.45	.52	−.23	.67
Old wasps	.06	.79	.46	.99	.08	−.09	−.10	.88	.27	.69	.09	.17
Middle-aged wasps	.86	.13	−.12	.89	.37	−.14	.09	.11	.95	.92	−.16	−.25
Young wasps	.79	−.09	−.08	.74	.58	.26	.89	.25	.19	.90	.36	.21
Pupae	.26	.27	−.09	.31	.82	.16	.50	.74	.16	.70	.07	.37
Hatched cells	.17	.92	.12	.74	.20	.60	.42	.76	.14	.81	.53	.23
New cells	.90	.13	.08	.28	.90	−.04	.68	.14	.64	.84	−.17	.28
E. polistis	−.05	.08	.97	−.05	−.17	−.88	.95	.07	−.15	.04	−.35	−.81
C. iphitalis	−.16	.87	−.33	−.38	−.48	.72	−.03	.33	.70	−.23	.91	.11
Eigenvalue	4.37	2.27	1.35	6.32	2.03	1.50	5.27	2.60	1.21	5.87	2.15	1.15
% variance explained	39.7	20.6	12.3	57.4	18.5	13.7	47.9	23.6	11.0	53.4	19.6	10.5

Presence of intermediate egg-layers may be evidence of a weak queen and a correspondingly smaller nest, causing intermediate egg-layers not to load positively on the first component. Parasitism may be a random event dependent on nest discovery by individual parasitoids so parasitism also does not load positively on the first component in June or July. In September the first component no longer encompasses only nest size. Nest size and nest decline are combined in September. By this time a nest is more likely to have been encountered by a moth at some time, since the nest has been present so long. Therefore, the ability of moths to exploit larger nests more heavily is reflected in the first component, whereas it was not so earlier in the season. Likewise those nests that have been there from the beginning of the season are not only likely to be largest, but also to have more hatched cells than new cells. Nests built after the beginning of the season as replacements to nests that were knocked down, or new satellites, are likely to be both younger and smaller; in this component, age and size are combined in September whereas they were separate earlier.

The second principal component differs in biological meaning across months, for both the nest analysis and the nest systems analysis. In June it is primarily a parasitism component, strongly correlated with both *E. polistis* and *C. iphitalis* parasitism, explaining 14.9 percent of the variance. Numbers of intermediate egg-layers are also strongly correlated with this component, which is less easily related to parasitism except by the frequency with which nests with parasitism have intermediate egg-layers.

In July the second principal component is clearly a component of nest decline. Old wasps, hatched cells, and *C. iphitalis* parasitism all are strongly correlated with this component, as expected in a general decline. This component explains 16.4 percent of the variance.

In September the second component is the reverse of that in July. Whereas the second component in July loaded strongly on nest decline variables, the second component in September is most strongly correlated with nest growth variables, egg-layers, young wasps and new cells, explaining 17.8 percent of the variance. This reversal in components is consistent with the fewer numbers of growing nests in September, while in July, fewer nests are declining. In September therefore growth is the component uncorrelated with nest size, the first component; in July decline is uncorrelated with nest size.

In June the only way to distinguish between nests other than the first component of general size is by presence of parasitism. By July and September, general differences in nest age are apparent, and declining nests are distinguished from growing nests. The association between variables is thus more constant in July and September than it was in June.

The third principal component, while significant, has no clear biological meaning in June or September; in July it separates those nests with egg-layers from those with intermediate egg-layers. In the systems sample it separates those nests parasitized by *E. polistis* from all other nests.

Size is the most important nest characteristic, explaining over a third of the variance in each sample. The second component, dependent on season, either involves parasitism or the dynamic nest condition (decline or growth).

The second part of this analysis compares principal components calculated separately for independent nests, main nests, satellite nests, and satellite nest systems in June and July (Table 3). The biological meaning of the components varies among nest types.

The first principal component for independent nests in June is nest size, explaining 37.9 percent of the variance. The second component for this sample is nest parasitism by both *E. polistis* and *C. iphitalis*, explaining 16.9 percent of the variance. Independent nests also possess a biologically real third component, the presence of either an intermediate or a full egg-layer, that explains 10.1 percent of the variance.

Main nests in June have only two biologically meaningful components: the first and third. The first is nest size, the third, nest parasitism, so these are the same as the first and second components of independent nests. When satellite nests are considered in June, the first component combines the characteristics of nest size, decline and parasitism. This indicates that larger satellites are probably older than smaller satellites, and more heavily parasitized. In satellite nests alone parasitism is associated with decline whereas for main nests and independent nests parasitism has not yet been associated with decline. The older, more homogeneous populations of main nests and independent nests are less variable than the population of satellite nests.

Satellite nests are initiated only a few weeks before the June collections. Since the two most important components for main nests and independent nests (nest size and nest parasitism) are the same at this time, differences between those nests that initiate satellites and those that do not are differences in quantitative values for the first two components, and not differences in the associations between variables. Supporting this result is the fact that in single variable comparisons, main nests have been found to be consistently larger than independent nests, but not more parasitized (Strassmann, in prep.).

In satellite systems in June, as in main nests and independent nests, the two meaningful components are nest size and parasitism, explaining 53.2 and 20.6 percent of the variance, respectively.

In July the biologically real principal components are those of size, growth, decline, *E. polistis* parasitism and a separation of *C. iphitalis* from *E. polistis*. Again there are quite a few differences in principal components among the samples. In independent nests in July, the first component is nest size and growth and accounts for 39.7 percent of the variance. The second principal component is nest decline and *C. iphitalis* infestation, which accounts for 20.6 percent of the variance. The third principal component is *E. polistis* parasitism and accounts for 12.3 percent of the variance.

In the sample of main nests in July the first principal component is nest size accounting for 57.4 percent of the variance. The second principal component combines nest growth with nest size and explains 18.5 percent of the variance.

Correlations among the variables for satellite nests in July were so low that no principal components were biologically interpretable.

Satellite systems possessed only one clear component, that of nest size, which accounts for 53.4 percent of the variance.

There is a difference between independent and main nests in July for the first two principal components. The first component for independent nests associates nest growth with size while the first component for main nests is still nest size alone. By definition main nests possess satellites. At this time additional nest growth is probably taking place on the satellite and not on the main nest, whereas the larger independent nests are still growing. It follows that, for independent nests, the second component is nest decline (and *C. iphitalis*), while for the main nests it is nest growth (and size).

Most of the first three significant principal components in this analysis were also assigned a logical biological meaning (Table 4). The four basic component patterns, nest size, growth, decline and parasitism, are of central importance to the nesting biology of polistine wasps, and are by nature multivariate (Table 1). However, principal components analysis is not usually used to handle them. Proportions, such as new cells to total cells for a measure of nest growth are more typically used, but a proportion is only valid as a new variable when the coefficient of variation of the numerator and denominator are the same (Tanner, 1951).

Table 5 presents the coefficients of variation [(S.D. $\times$ 100)/$\bar{x}$] of the 11 variables in the three collections. The coefficient of variation of any given variable is fairly consistent from June to September but there are great differences among variables (Table 5). The coefficients of variation of quantitative measures are typically between 5 and 10 (Simpson, Roe and Lewontin, 1960). By comparison the values in Table 5 are very high. Any new variables created from proportions of any two of these variables will overemphasize the variable with the higher coefficient of variation (Tanner, 1951). Of course this can be corrected by using Z-scores (Tanner, 1951). Where a trait is expressed as a significant principal component, analysis can proceed based on the principal components. Principal components provide unbiased weighting of variables into uncorrelated components. Components that are the same across samples may thereby be treated as new variables, and as such, may be compared between populations. For example, in those samples where nest size is the first component, it explains 38 to 57 percent of the variance. Comparing this component between samples makes more

Table 4. Biological meaning of principal components in each sample.

a. All nests

Principal components	June	July	September
1.	Nest size	Nest size	Nest size with decline + *C. iphitalis*
2.	Nest parasitism	Nest decline + *C. iphitalis*	Nest growth
3.	—	Separates nests with intermediate egg layers from nests with full egg layers	—

b. Nest systems

Principal components	June	July
1.	Nest size	Nest size
2.	Nest parasitism	*C. iphitalis*, nest decline
3.	—	*E. polistis*

c. June

Principal components	Independent nests	Main nests	Satellite nests	Satellite system
1.	Nest size	Nest size	Nest size, decline and parasitism	Nest size
2.	Nest parasitism	—	—	Nest parasitism
3.	Nests with intermediate or full egg layers	Nest parasitism	—	—

d. July

Principal components	Independent nests	Main nests	Satellite nests	Satellite system
1.	Nest growth and size	Nest size	—	Nest size
2.	Nest decline + *C. iphitalis*	Nest growth and size	—	—
3.	*E. polistis*	—	—	—

Table 5. Coefficients of variation (C.V.) and standard errors of the coefficients of variation (S.E.) for all nests in June, July and September.

	June (75)		July (41)		September (32)	
	C.V.	S.E.	C.V.	S.E.	C.V.	S.E.
Non egg-layers	90	11.9	79	13.1	103	22.7
Intermediate egg-layers	203	50.4	147	37.4	237	103.6
Egg-layers	116	18.2	93	17.0	215	86.0
Old wasps	79	9.7	69	10.6	109	25.0
Middle-aged wasps	142	26.0	102	19.8	108	24.6
Young wasps	176	38.5	120	26.1	178	60.3
Pupae	119	19.0	94	17.3	186	65.4
Hatched cells	93	12.5	105	20.8	121	30.0
New cells	79	9.7	76	12.3	72	12.8
E. polistis	381	170.5	306	150.1	265	128.5
C. iphitalis	220	58.7	173	50.5	175	58.4

complete use of the data available than does comparing any one of the individual variables associated with nest size. More precise distinctions between populations may thus be made.

In a number of samples the second component is nest parasitism. In these cases parasitism may be compared across samples by comparing the second component. This has the advantage of eliminating the effects of nest size, but the slight positive loading of non-parasitism variables on this component may dilute the meaning that can be assigned to the component.

The components that appear as combinations of biologically interpretable variables may be compared between samples for qualitative changes in the identity of the component, but not for quantitative differences in a given trait. Changes in associations among variables into different biologically interpretable components provide valuable information on both differences among nest types and among nest types at different times of the season. Eleven nest variables considered here resolved into four biologically significant types of principal components. These components differ somewhat among different chronological samples and different nest types in ways that can be explained biologically.

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