References and Notes

1. D. Cohen, *Science* **161**, 784 (1968).
2. ______, *ibid.* **175**, 664 (1972).
3. ______, *IEEE Trans. Magn.* **11**, 694 (1975); since completing our work we were informed of a related publication (T. J. Teyler, B. N. Cuffin, D. Cohen, *Life Sci.*, in press).
4. Ongoing and visually evoked fields have also been observed in a magnetically shielded environment by M. Reite, J. E. Zimmerman, J. Edrich, J. Zimmerman (in preparation).
5. A. H. Silver and J. E. Zimmerman, *Phys. Rev.* **157**, 317 (1967); J. E. Zimmerman, P. Thiene, J. T. Harding, *J. Appl. Phys.* **41**, 1572 (1970).
6. We use a thin film bridge type of SQUID and r-f-shielded Dewar (Superconducting Technology, Inc., Mountain View, Calif.), together with SQUID electronics with 19 Mhz r-f bias (S.H.E. Manufacturing Corp., San Diego, Calif.).
7. J. E. Opfer, *IEEE Trans. Magn.* **9**, 536 (1974); D. Brenner, S. J. Williamson, L. Kaufman, in *Proceedings of the 14th International Conference on Low Temperature Physics*, M. Krusius and M. Vuorio, Eds. (North-Holland, Amsterdam, 1975), vol. 4, p. 266.
8. "Relative power" on the axes of Fig. 2, C and D, refers to the mean square observed field. The ratio of the mean square field of the response to the mean square field obtained on noise trials is equivalent to the F ratio of classical statistics. For these figures, 500 sweeps at twice the stimulus period, used in signal averaging, correspond to 500 degrees of freedom; therefore $F > 1.2$ has a probability $P < .01$ of occurring if only noise is present. Responses with a power greater than 65 are considered highly significant.
9. M. Clynes and M. Kohn, *The Evoked Potentials* (Elsevier, Amsterdam, 1967), p. 82.
10. This work was supported by the National Science Foundation, the National Institutes of Health Biomedical Sciences support grant to New York University, and the New York University Arts and Science Research Fund. We thank D. Cohen and W. S. Goree for their useful comments and suggestions.

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Multidimensional Variation in an Avian Display: Implications for Social Communication

Abstract. *An analysis of song-spread displays performed in social communication by carib grackles,* Quiscalus lugubris, *revealed that two components of this motor coordination, beak elevation and wing elevation, varied independently. Variation in each depended strongly on the performer's social context, an indication that these components simultaneously reflected different behavioral tendencies of the performer. Independent variation in the elements of a display can permit transmission of more information per display about the performer's behavioral state.*

Male and female carib grackles, *Quiscalus lugubris*, perform a complex coordination, the song-spread display, both when courting the opposite sex and when near rivals of the performer's own sex. Early ethologists recognized the importance of such discrete classes of actions in the social behavior of many animals. These action patterns sometimes attain surprising degrees of stereotypy in repeated performances by one individual or within a population, although most vary substantially in both respects (*1–3*). Because many of these discrete action patterns serve primarily for communication with social partners, the variation or stereotypy in displays requires examination in the framework of the species' requirements for social communication.

The information available to social partners will depend in part on the variability of an action pattern and on the covariation of its elements with the performer's behavioral tendencies, as indicated by the social circumstances or by preceding and following actions (*4*). This report, a multivariate analysis of a communicatory display, documents for the first time an action pattern with independently varying components, each associated with different social contexts. This evidence suggests that patterns of variation in this display increase the information available about the performer's behavioral state.

The carib grackle's song-spread display, probably homologous with similar displays of related species, such as the familiar common grackle, *Q. quiscula* (*5*), involves synchronized movements of all of the animal's extremities. It comprises at least eight motor elements (Fig. 1): (i) a vocalization, (ii) dorsad rotation of the cranium so that the beak is lifted, (iii) elevation and slight extension of the wings, (iv) rapid fluttering of the wings in periodic bouts, (v) dorsad rotation of the deeply keeled tail so that the outer edges of the tail slightly pass vertical, (vi) alternating extension and flexion of the legs to impart a bouncing motion to the body, (vii) irregular movements of the gray nictitating membrane across the yellow iris, and (viii) partial erection of the ventral and anterior contour plumage. The last seven components all vary considerably from performance to performance by the same individual, to the extent that this variation greatly exceeds any consistent differences between individuals. The observations reported here pertain to performances by a number of individuals in one nesting colony. The position of the tail during the display varied considerably less than did the orientation of the beak and the movements of the wings. Consequently, the following discussion primarily deals with variation in the elevation of the beak and wings. Females performed song spreads much less frequently than did males.

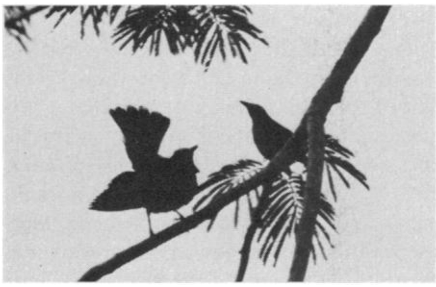

Fig. 1. Male carib grackle performs a song-spread display (left) while facing another male in a weak version of the bill-up display (right). Photographed at Fundo Pecuario Masaguaral, Guárico, Venezuela.

For these studies I observed male and female grackles from distances of 5 to 10 m while they displayed on the low branches of an isolated tree used by the grackles for nesting. The study was conducted 3 km west of Arima, Trinidad, West Indies, in July 1971. For every song spread observed in clear view during hour-long watches, I systematically dictated the performer's sex, the maximum wing elevation (in intervals of 15° above the resting position), the maximum beak elevation (in intervals of 10° with respect to horizontal), the performer's social context (whether a male, a female, or no other bird was less than 1 m away), and temporal context (whether or not the bird performed bill-up displays, indicative of aggressive tendencies, immediately before or after the song spread). I was close enough to the displaying grackles to see the movements of the beak and wings clearly. In any one minute, I recorded data only once from the same individual.

These observations allowed me to determine the frequencies with which each sex performed song-spread displays with different combinations of beak elevation, wing elevation, social context, and temporal context. Because the extremes of either beak or wing elevation occurred relatively infrequently, for the following analyses I condensed each of these parameters into two classes, higher and lower elevations, divided as near the median as possible (*6*). The complete data for song-spread displays by each sex thus constituted a contingency table in four dimensions: beak and wing elevation (each with two categories), social context (with three categories), and temporal context (with two categories).

To test for associations among beak elevation, wing elevation, and social context in males' displays, I required a nonparametric analysis of independence for the corresponding three-dimensional (2 by 2 by 3) matrix, for which the G statistic provides an appropriate procedure (*7*). A three-way analysis with the G statistic established, with negligible chance of error, that these three variables lacked joint independence (Table 1). The levels of both beak and wing elevation depend strongly on social context. These two elements of the song-spread display, however, varied independently, regardless of social context.

Table 1. Three-way analysis of independence of beak elevation (BE), wing elevation (WE), and social context (SC) in song-spread displays by males ($N = 115$); d.f., degrees of freedom.

Variables	Test	G	d.f.	P
BE × WE × SC	Independence	25.84	6	< .001
BE × WE	Independence	0.40	1	> .5
BE × SC	Independence	12.80	2	< .01
WE × SC	Independence	9.93	2	< .01
BE × WE × SC	Interaction	2.70	3	>.2

Table 2. Comparison of social contexts, taken two at a time, for differences in beak angles and wing angles in song-spread displays by males. Each G statistic is for a 2 by 2 contingency table for two social contexts and two classes of beak or wing elevation.

Beak angle				Wing angle			
Null hypothesis	P	G	N	Null hypothesis	P	G	N
Near female = alone	> .5	0.36	60	Near male = alone	> .8	0.02	89
Near male = near female	< .01	9.64	81	Near female = near male	< .02	6.10	81
Near male = alone	< .01	7.24	89	Near female = alone	< .05	4.42	60

The data reveal that elevation of the beak is more prominent when a displaying male is near another male, while elevation of the wings is more prominent when a displaying male is near a female. Higher elevation of the beak, owing to its similarity in form to the bill-up display, probably reflects stronger agonistic tendencies in males, and thus beak elevation is understandably more pronounced when males are close together.

Two-way comparisons of social contexts (Table 2) showed that the distribution of beak angles was similar when males performed near females or alone. Hence the higher beak elevations near other males evidently resulted from elicitation of this variant by nearby males, rather than inhibition of beak elevation by nearby females. Similarly, the distribution of wing angles was similar when the male performed near a male or alone. Evidently, higher wing elevation was evoked by proximity to a female, rather than inhibited by proximity to another male.

The occurrence of bill-up displays shortly before or after the song-spread display was associated with higher beak elevations during song spread, although this trend reached statistical significance only when the male displayed alone or near a female ($G = 4.40$, $P < .05$, $N = 60$). Males displaying near other males evidently raised their beaks, regardless of whether they performed agonistic displays such as the bill-up ($G = 0.74$, $P > .3$, $N = 55$). The occurrence of bill-up displays had no significant influence on wing elevation during song spreads ($G = 2.02$, $P > .1$, $N = 115$). When the performer was near a female, there was a trend toward reduced wing elevation in song spreads associated with bill-up displays, but these displays occurred so infrequently in this social context that reliable conclusions are not possible.

My data on song spreads performed by females when alone show that their beak elevations, but not wing elevations, were significantly higher than in displays performed by males alone. I observed too few displays by females in other social contexts to allow analysis, although my few observations suggest that elevation of the beak was even higher when the female performs near a male. The female precopulatory display in many passerine birds involves dorsad rotation of the cranium, so that increased beak elevation in female song-spread displays might indicate increased sexual tendencies. Beak elevation thus might indicate different behavioral tendencies in males and females.

This study has revealed that the song-spread display is a unitary coordination only in the sense that certain classes of movements of the extremities are triggered nearly simultaneously. Once triggered, the beak and wing movements, at least, require separate control.

The separate associations of each element with distinct social and temporal contexts suggest that they vary with different behavioral tendencies of the displaying male. It has been suggested that the elements of certain action patterns might correlate with different behavioral tendencies of the performer, for example, tendencies to escape, attack, or perform sexual behavior (*3, 8*). In any one context, such tendencies, or elements that reflect them, are not necessarily independent variables. However, displays that include independently varying elements have the potential for conveying more information about the animal's behavioral state than do those with covarying elements.

The information in a display about the performer's behavioral tendencies depends on the multivariate frequency distribution of individuals' behavioral tendencies in a specified context and on their combination in controlling each component of the display. A display with two components, for instance, includes maximum information about the performer's tendencies in a particular context when the components reflect those orthogonal combinations associated with most of the variance. Whenever natural selection favors signals with maximum information about behavioral tendencies, we might thus expect the elements of communicatory displays to have low covariation. In other situations, natural selection might favor redundant signals, with covarying components, to minimize errors in communication, even at the expense of encoding less information at one time about at least some of the signaler's behavioral tendencies. Previous studies have provided a few examples of both sorts of variation in communicatory displays (*2, 3*). The present study is the first to document a display with independent variation of two components and to provide initial evidence that these components reflect different behavioral states of the signaler.

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References and Notes

1. B. Dane, C. Walcott, W. H. Drury, *Behaviour* **14**, 265 (1959); P. Marler and D. Isaac, *Condor* **62**, 124 (1960); G. W. Ferguson, *Syst. Zool.* **19**, 79 (1970); S. J. J. F. Davies, *Behaviour* **36**, 187 (1970); B. A. Hazlett, *ibid.* **42**, 270 (1972); T. A. Jenssen, *Copeia* (1971), p. 197; W. M. Schleidt and M. D. Shalter, *Z. Tierpsychol.* **33**, 35 (1973); R. H. Wiley, *Behaviour* **47**, 129 (1973); W. M. Schleidt, *Z. Tierpsychol.* **35**, 184 (1974).

2. J. A. Stamps and G. W. Barlow, *Behaviour* **47**, 67 (1973).

→. A. W. Stokes, *Behaviour* **19**, 118 (1962).

4. P. Marler, *J. Theor. Biol.* **1**, 295 (1961); in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart and Winston, New York, 1965), pp. 544–584; S. A. Altmann, in *Social Communication among Primates*, S. A. Altmann, Ed. (Univ. of Chicago Press, Chicago, Ill. 1967), pp. 325–362; W. J. Smith, in *Animal Communication*, T. A. Sebeok, Ed. (Indiana Univ. Press, Bloomington, 1968), pp. 44–60; S. Green, in *Primate Behavior*, L. A. Rosenblum, Ed. (Academic Press, New York, 1975), vol. 4, pp. 1–102.

→ R. W. Ficken, *Auk* **80**, 52 (1963); R. H. Wiley, *Anim. Behav.*, in press.

6. Classes of beak elevation: angles less than 10° above horizontal ($N = 57$); and angles 10° or greater ($N = 58$). Classes of wing elevation: angles less than 45° from vertically downward ($N = 89$); and angles 45° or greater ($N = 26$). These criteria divided the numbers of observations as near the respective medians as possible. The frequency distributions of beak and wing angles as originally recorded, in 10° and 15° intervals, respectively, were unimodal for each social and temporal context.

7. R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), pp. 601–607.

→ N. Tinbergen, *Behaviour* **15**, 1 (1959); P. Leyhausen, *Z. Tierpsychol. Beih. 2* (1956); R. A. Hinde, *Animal Behaviour* (McGraw-Hill, New York, ed. 2, 1970), pp. 373–377.

9. Supported in part by a grant from Sigma Xi, NIMH grant MH 22316, and NIH postdoctoral traineeship GM01789 at Rockefeller University. I thank M. S. Wiley for essential assistance in the field and for help with analysis of the data; V. D'Arceuil for permission to work on La Florissante Estate, D'Abadie, Trinidad; the University of the West Indies, St. Augustine, Trinidad, for accommodations; and P. Marler, W. Schleidt, and C. Hopkins for suggesting important improvements in the manuscript.

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