THE INFLUENCE OF VOCAL BEHAVIOR ON THE PERFORMER'S TESTICULAR ACTIVITY IN BUDGERIGARS (*MELOPSITTACUS UNDULATUS*)

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A striking feature of an aviary containing the Budgerigar is the seemingly constant "chatter" or "singing" which results from many individuals simultaneously performing Loud and Soft Warble. Both of these "songs" (sensu Borror, 1961) contain several components performed in varying sequences and are the most elaborate of all Budgerigar vocal patterns (for description of all vocalizations, see Brockway, 1964*a* and 1964*b*).

It is common avicultural knowledge that Budgerigars (commonly called parakeets in the U.S.A.) typically do not breed unless pairs can hear each other. This has been experimentally substantiated by Ficken et al. (1960) and Brockway (1964*c*). When males are able to hear others, individuals commonly spend up to one-quarter of their waking hours performing Loud Warble as a result of inductive mimesis (Brockway, 1964*b* and unpublished data). If permitted to interact with a homo- or heterosexual partner, such males will also perform three precopulatory vocalizations, namely Soft Warble, Tuks, and Whedelees. These three vocal patterns function in part to stimulate ovarian activity (Brockway, 1965). Even without a sexual partner, males that are able to hear others maintain their year-long typically high levels of testicular activity and can be milked for motile, unstainable spermatozoa (see Table 1). Males, which are prevented from hearing each other, perform such vocalizations as alarm and location calls in quantities similar to those of males able to hear others. Such isolated males, however, perform significantly little or no Loud Warble or precopulatory sounds, cannot be milked for seminal fluid containing spermatozoa, and possess markedly regressed testes and vasa deferentia after 3 to 5 weeks of isolation (Brockway, 1964*c* and Ficken et al., 1960).

To investigate whether it is the *hearing* of Loud Warble with or without precopulatory vocalizations performed by other males and/or some factor arising from the *performance* of these by an individual which stimulates a male's testicular activity, the gonadal conditions of both "devocalized" and sham-operated males able to hear others was studied.

MATERIALS AND METHODS

Seven males were rendered incapable of performing recognizable budgerigar sounds by surgically severing their right and left sternotrachialis muscles and removing a half-inch segment from both the right and left hypoglossal

nerves adjacent to these muscles. Such "devocalized" birds utter only hoarse mono- and polysyllabic "burp" or "keek" sounds. Sham operation on seven control birds involved procedures identical to those used in "devocalization" except the sternotrachialis muscle and hypoglossal nerves were only gently touched with forceps. For further control, "devocalization" surgery was performed on only the left side of two additional males.

At the time of surgery (day 0) and at 21 and 36 days later, all of the sexually mature 9 month old virgin males used for this study were milked for spermatozoa and laparotomized so that their reproductive organs could be measured. Following the initial surgery, all males were returned to the aviary environment in which they had previously lived and where they could hear all budgerigar sounds including the almost continual daily Loud Warble performed by some 60 males in stock cages and 14 males of pairs in breeding cages.

Control and experimental males were placed in adjacent cages so that both groups could hear the abnormal utterances of "devocalized" males. The sounds produced by each "devocalized" or control male were qualitatively and quantitatively recorded during 45 minute observation periods three to six times a week for 35 days. Maintenance (e.g.; preening, eating, etc.) and sexual behavior were noted during these observations and also at other times during the study.

French's Parakeet Seed, French's Conditioning Food, cuttlebone, quartz gravel, and water were provided ad libitum.

RESULTS AND DISCUSSION

After three days, all control birds resumed their typical performance of budgerigar sounds including large quantities of Loud Warble. The seven "devocalized" males continued to perform only low-pitched "burp" or higher-pitched "keek" sounds throughout the study. The results, presented in Table 2, show that high levels of testicular activity are maintained only by males performing typical budgerigar sounds. Hearing the vocalizations of other males is not sufficient. No finer correlation was found between the recorded amounts of any vocalization performed by an individual and the size of his reproductive organs within either the control or experimental groups. That surgical trauma did not produce the decreased testicular activity of the "devocalized" males can be seen from data on controls, especially those "half-devocalized" birds which showed no significant changes in testicular activity and performed Loud Warble and all typical adult non-sexual vocalizations.

"Devocalized" birds experience two phenomena which control birds do not. They suddenly (1) are unable to perform normal species-typical vocal

TABLE 1

EFFECT OF INTRASPECIFIC VOCAL STIMULI FOR 35 DAYS UPON TESTICULAR ACTIVITY OF ADULT MALE BUDGERIGARS.*

Males	No.	Mean testis length (mm)			Mean testis width (mm)			Mean vasa deferentia diameter (mm)			No. of males showing spermatozoan upon milking			Mean stage of spermatogenesis****
		Day-1**	Day-35	P***	Day-1	Day-35	P	Day-1	Day-35	P	Day-1	Day-35	P	Day-35
Can hear others	24	7.35	8.68	<0.005	4.75	5.10	>0.20	1.00	1.00	>0.20	24	24	–	7.00
Isolated	12	7.46	4.39	<0.005	4.79	2.42	<0.005	1.00	0.37	<0.005	12	22	–	3.08
P***		>0.20	<0.005		>0.20	<0.005		>0.20	<0.005		–	<0.005		<0.005

* All males, 1 to 2 years old, were caged with a mate and performed similar amounts of all budgerigar vocalizations except Loud Warble or precopulatory vocalizations. Each isolated male could hear no other male and performed virtually no Loud Warble or precopulatory vocalizations.

** Prior to experimentation; when all males, caged under typical aviary conditions, could hear others.

*** Data were evaluated by analysis of variance tests (Li, 1964).

**** Scored on histological preparations by the system used by van Tienhoven et al. (1956).

TABLE 2
STIMULATION OF TESTICULAR ACTIVITY BY FACTORS INVOLVED IN PERFORMING VOCAL BEHAVIOR.*

Treatment of males	Mean values for: Testis length (mm) on day				Testis width (mm) on day				Vasa deferentia width (mm) on day				Number of males showing spermatozoan upon milking, on day			
	0**	21	36	P(0/36)***	0	21	36	P(0/36)	0	21	36	P(0/36)	0	21	36	P(0/36)
Devocalized	6.71	3.21	3.79	<0.005	3.93	1.79	2.29	<0.005	1.04	0.41	0.43	<0.005	7	0	0	<0.005
Sham-operated	7.50	6.82	7.36	>0.20	4.46	4.04	4.36	>0.20	1.04	0.98	1.09	>0.20	5	6	6	>0.20
Half-devocalized****	(7.75	7.75	8.00)		(5.00	5.50	5.37)		(1.16	1.16	1.16)		(2	2	2)	
P	>0.20	<0.005	<0.005		>0.10	<0.005	<0.005		>0.20	<0.005	<0.005		>0.10	<0.005	<0.005	

	Changes in testis lengths per individual between days		Changes in testis widths per individual between days		Changes in vasa deferentia widths per individual between days	
	0–21	0–36	0–21	0–36	0–21	0–36
Devocalized	–3.21	–2.64	–2.14	–1.64	–0.62	–0.61
Sham-operated	–1.07	–0.18	–1.07	–0.64	–0.11	–0.06
P	<0.005	<0.005	<0.05	<0.05	<0.005	<0.005

* All males heard all vocalizations including extensive Loud Warble from 60 non-paired and 14 heterosexually paired males both before and during study. Only sham-operated and "half-devocalized" males performed any Loud Warble or precopulatory vocal patterns. Data were evaluated by Chi-square and analysis of variance tests.

** The day of surgery, 1 day before the start of this study.

*** Comparisons between values for day 0 and 36.

**** These values are not included in the statistical comparisons between devocalized and control sham-operated males.

behavior and (2) produce sounds dissimilar to any they had previously made. These experiences cannot, as yet, be separated from each other. Furthermore either, in itself, might be a stress sufficient to prompt the decreased testicular activity observed for "devocalized" males. This possibility might be minimized by "devocalizing" young birds well before they ordinarily would perform the elaborate Loud Warble and precopulatory vocalizations and studying their subsequent gonadal development. High blood levels of adrenal hormones (e.g., corticosteroids) are commonly associated with stress, resulting in gonadal regression. Unfortunately, methods do not yet exist for measuring these levels in the limited blood volumes of small birds. Accordingly, birds were examined for other, grosser indications of stress. The following data suggest that the "devocalized" males were *not* undergoing reactions to stress as a result of their inability to perform anything but abnormal vocalizations: (1) the amounts of food and water they consumed did not differ from the amounts consumed by the control group; (2) their body weights were insignificantly different from those of the controls; (3) they showed no abnormal persistently ruffled or sleeked body feather postures; (4) they performed no aberrant visible behavior patterns; (5) some males performed visible precopulatory displays oriented to other males (a typical event among unisexually caged Budgerigars); and (6) 70 days after devocalization, their reproductive organs were in the same conditions as noted 35 days after "devocalization."

Of all the vocalizations in the repertoire of *Melopsittacus*, only Loud Warble, Soft Warble, Tuks, and Whedelees appear to be associated with gonadal activity (Brockway, 1964*c*). Not all control birds were heard to perform the three precopulatory vocalizations and yet all non-performers showed spermatozoa when milked and there was no distinguishable difference in their testes and vasa deferentia measurements and those of control males which did perform these vocalizations. Furthermore, the circumstances during which these three vocalizations are predominantly performed, i.e., precopulatory interactions, are not necessary for the full gonadal development or function of either sex (Brockway, 1962 and 1965). These observations strongly suggest that the performance of Loud Warble promotes the maintenance of high levels of testicular activity.

Whilst hearing the vocalizations of other males appears insufficient, in itself, to maintain full testicular activity, a male's performance of Loud Warble stimulates and in turn is stimulated by the Loud Warble of others. By so stimulating individual vocal performances, social vocal activity would play an important role in promoting the testicular activity of the flock. This would also help to explain why a male which is isolated from the sounds of others typically shows low levels of androgen secretion and spermatogenesis

and why pairs of Budgerigars isolated from the sounds of others typically fail to breed.

Other known instances in which the performance of specific behavior patterns stimulates or is required for anterior pituitary gonadotrophin or gonadal hormone secretions *in the performer* seems mainly restricted to parental behaviors (for review, see Lehrman, 1961). Other known examples of a behavior's stimulation of anterior pituitary or gonadal activity involve sexual or courtship interactions between 2 individuals. In these, the behavior of one influences the endocrine activity of the other (e.g., Brockway, 1965; Burger, 1942 and 1953; Polikarpova, 1940; Matthews, 1939; Shoemaker, 1939; Lehrman et al., 1961, and Warren and Hinde, 1961). Thus, this study on Budgerigars may be the first experiment indicating a self-stimulation of an individual's gonadotrophin secretion or gonadal activity by the performance of a non-parental behavior. It would be interesting to know if any "songs" of other avian species might have, in part, a similar function.

Another point of interest stems from the ethological designation of all vocal behaviors as displays. Displays are commonly regarded as those species-typical behavior patterns primarily functioning to provide signals which alter the activity of the nervous or endocrine systems of other individuals (Tinbergen, 1964; and Hinde and Tinbergen, 1958). Budgerigars may possess at least one display which functions not only to stimulate other males to perform it but also stimulates the endocrine activity of the performer.

SUMMARY

Data on surgically "devocalized" and sham-operated controls indicates that the gonadal activity of male Budgerigars may be stimulated as a result of their performance of vocal display(s) rather than as a result of hearing such behavior by others. This may be the first demonstration of the self-stimulation of an individual's endocrine activity by his performance of a species-typical behavior which involves gonadotrophins and non-parental behavior. Since vocalizations are ethologically regarded as displays, the current thinking about the functions of displays may need expansion.

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