

observations. Reviewer S. M. Russell commented on a later draft, as did M. Alvarez del Toro, who called my attention to the Chiapas specimen. J. V. Remsen provided many useful data on specimens under his care at the Louisiana State University Museum of Zoology, as did R. W. Storer on specimens at the University of Michigan Museum of Zoology. Much of my field work in Mexico was supported by the Welder Wildlife Foundation, with additional support from the National Audubon Society and the U. S. Fish and Wildlife Service. I thank K. F. Lueder of Chapala, Jalisco, for his hospitality during the course of much of my field work.

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EFFECT OF MATE LOSS ON SONG PERFORMANCE IN THE PLAIN TITMOUSE

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Past studies on titmice have found song to serve exclusively in defense of territory (e.g., Dixon 1949, Lemon 1968, Krebs et al. 1978), yet Krebs et al. (1981) showed that in the Great Tit (*Parus major*) song may also function to attract females. They noted that after a female was removed from a mated pair, the male increased song output almost six-fold and, when reunited with the female, subsequently decreased his singing.

While studying the singing behavior of the Plain Tit-

mouse (*Parus inornatus*), I observed a similar but natural experiment when two males lost their mates. In this note I describe the changes in singing behavior of these males and discuss their significance concerning the roles of song in parids.

The study population was located 22 km N of Flagstaff, Arizona in a pinyon-juniper-ponderosa pine ecotone. In 1982, five males and some females were marked with U.S. Fish and Wildlife Service aluminum bands and unique combinations of colored plastic leg-bands. Birds were observed between 06:00 and 12:00 usually for a period of one hour per day several times a week. Observations were made from early March through late May. Songs, behavioral observations, and timing (from running stopwatches) were recorded simultaneously on a Uher 4000 Report IC tape recorder with a Dan Gibson parabolic microphone.

This report deals with the behavior of four territorial males, all of whom were mated at the beginning of the

breeding season and were synchronized relative to the stage of the breeding cycle. Male 54 lost his mate on 19 May; monitored for 10 days, he was found to remain unmated. A second bird, Male 58, appeared to behave like a normal, territorial, mated male although I did not measure his singing behavior until he lost his mate. On 20 May, I heard an abnormally large amount of song from his territory. I observed him for 3 h that day and on the nine days following; during this time I never saw him with a female. The singing behavior of these two now unmated males was compared to that of two mated "controls," Males 49 and 55, who remained paired for the entire breeding season.

Four parameters of singing behavior were chosen for comparison: (1) the number of bouts sung per hour, (2) performance time or the number of seconds spent singing per hour, (3) average bout length and (4) "total" song bout versatility. Versatility is a measure of the variance of song output (Hartshorne 1956): in this case, the use of different song types by a bird. Plain Titmice in my population have an average of 12 different songs in their repertoire. A highly versatile bout has a number of different song types and/or a number of switches between unlike songs. "Total" versatility is computed by multiplying (a) the number of different song types in a bout by (b) the number of transitions between unlike songs for that bout (Kroodsmma and Verner 1978).

To examine the difference in singing behavior in mated birds and those that had lost their mates, I made the following comparisons. First, I used *t*-tests to test for the differences in the pre- and post-loss performance of Male 54. Second, I used analysis of variance to test for differences overall among Males 54 (post-loss only), 58, 55 and 49. If significant differences existed, a linear contrast test was used to test the hypothesis that the performance of the unmated birds as a group differed from that of the mated birds as a group. A Bartlett-Box test was used to test for homogeneity of variances in all comparisons.

All three parameters of song output increased significantly after Male 54 lost his female (Table 1). Analysis of variance also indicated significant differences among birds in all three parameters of song output. Linear contrast tests for all three parameters of song output indicated that the performance of the unmated birds differed from that of the mated birds (Table 2).

Versatility of bouts also increased with the loss of a mate (Fig. 1). Only 14.6% of the mated control birds' bouts and 10.3% of Male 54's bouts (when mated) showed some versatility (and these were low scores). This can be compared to the unmated males, 54 and 58, of whose bouts 44.4% and 50.5% were versatile. Thus, unmated males had a more variable output.

In addition to the changes in vocal behavior, I noted that at the onset of mate loss, both Males 54 and 58 seemed to be very agitated, continuously flying from one side of their territories to another. This behavior subsided somewhat after a few days.

Krebs et al. (1981) advanced three hypotheses to explain

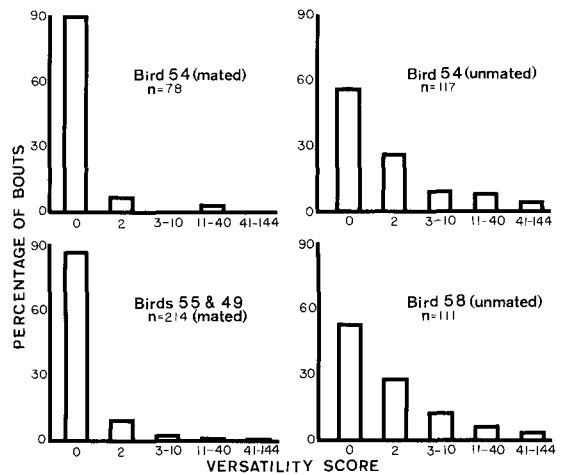


FIGURE 1. The distribution of bout versatility scores. For an explanation of versatility scores, see text. *n* = the number of bouts for which scores were calculated.

increased song output with the loss of a mate in the Great Tit; all could apply to the Plain Titmouse. First, a male may have to compensate for the absence of a mate by putting more effort into territorial defense. Both an increased song output and a more variable song output could be more effective in repelling rivals. I find this the least likely possibility, because (1) only males sing in long-range territorial defense, (2) during face-to-face encounters with other pairs, females rarely participate in any aggressive interactions (pers. observ.) and (3) at the time Males 54 and 58 lost their mates, other pairs were incubating eggs and very few territorial disputes were occurring.

Second, if a male sings in order to keep in contact with the female, in her absence he may increase his output in order to find her. Although most intra-pair contact is maintained through countercalling, this explanation is supported by observations on Male 54. During the first few days after losing his mate, Male 54 brought caterpillars and sang long bouts in the vicinity of the nest box. Before mate loss, he had used caterpillars in courtship feeding. Furthermore, the same box was used in a nest-site-selection ceremony with the female two days before she disappeared. It is questionable, however, why a male would persist in trying to find his old mate for 10 days or more.

Third, increased song output may aid in attracting a new mate. More singing may attract a new female first by increasing the chances that an unmated female will hear the male and secondly, the actual *level* of output may signal to a female that the male is unmated.

Increased bout versatility may also function to find the former mate, attract a new one, or both. High versatility may serve in a motivational, as opposed to a locational,

TABLE 1. Differences in the three parameters of song output for the pre-mate loss and post-mate loss periods for Male 54.

	Bouts/h		Performance time/h (s)		Bout length (s)	
	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD
Pre-loss period	19	4.32 ± 9.44	12	190.33 ± 705.85	60	49.07 ± 46.40
Post-loss period	9	16.33 ± 2.66	9	1,768.22 ± 586.48	60	86.92 ± 126.21
<i>t</i> statistic		17.135*		9.046		2.180
Significance		<i>P</i> < .001		<i>P</i> < .001		<i>P</i> < .032

* Non-homogeneity of variances required a separate variance *t*-test.

TABLE 2. Differences in the three song output parameters for the two unmated males, 54 and 58, and the mated controls, 55 and 49. *F* is for ANOVA, *t* is for linear contrast test.

Bird	Bouts/h		Performance time/h (s)		Bout length (s)	
	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD
54	9	16.33 ± 2.70	9	1,768.22 ± 586.48	60	86.92 ± 126.21
58	6	24.6 ± 4.05	6	2,186.50 ± 417.38	60	95.13 ± 102.96
55	22	7.95 ± 13.43	18	246.67 ± 296.06	60	44.58 ± 47.15
49	15	7.66 ± 5.08	8	481.13 ± 277.80	60	45.30 ± 51.82
<i>F</i> statistic	46.989		56.286		5.491	
Significance	<i>P</i> < .0001		<i>P</i> < .0001		<i>P</i> < .0012	
<i>t</i> statistic	11.306		12.195		4.026*	
Significance	<i>P</i> < .001		<i>P</i> < .001		<i>P</i> < .001	

* Non-homogeneity of variances required a separate variance *t*-test.

manner because it may be more physiologically stimulating to a female than low versatility (Kroodsma 1976). As with increased song output, increased versatility could in itself be a signal to a female that a male is unmated.

In conclusion, my study and that of Krebs et al. (1981) indicate that parids who are singing during the breeding season are not necessarily defending territories.

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