WHY DO BROWN TREMBLERS TREMBLE?

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Abstract.—The Brown Trembler (Cinclocerthia ruficauda), one of the endemic Mimidae of the Lesser Antilles, has a conspicuous and frequent habit of trembling its wings, the behavior for which it is named. Trembling consists of a perched bird drooping both wings 1-2 cm, then quickly raising them back to a normal position several times in rapid succession. Each "tremble" takes approximately 1 s. In this study, Brown Tremblers were observed and frequency of trembling was measured in March 1991, on Dominica. The rate of trembling was significantly different in different social contexts. Solitary, singing Brown Tremblers stopped singing and trembled at a mean rate of 1.74/min. Solitary Brown Tremblers that were foraging trembled at a mean rate of 6.8/min. Brown Tremblers foraging or traveling within 2 m of a conspecific trembled at a mean rate of 28.6/min, and Brown Tremblers involved in a rapid chase, <0.5 m apart, trembled at a mean rate of 50.0/min. Solitary Brown Tremblers (n = 31) show a significantly slower rate of trembling than social birds (two Brown Tremblers present, n = 13, P < 0.001, Mann-Whitney U-test, U = 43). The higher frequency of trembling in social contexts supports the hypothesis that trembling is a visual intra-specific signal. This interpretation is reinforced by data showing that Brown Tremblers almost always trembled immediately upon arriving at a new perch, and by the absence of a contact note used by Brown Tremblers.

¿POR QUÉ TIEMBLA CINCLOCERTHIA RUFICAUDA?

Sinopsis.—El temblador pardo Cinclocerthia ruficauda), uno de los Mimidae endémicos de las Antillas Menores, tiene el hábito de temblar de forma conspicua y frecuente sus alas, conducta a la cual debe su nombre. El temblar consiste en bajar ambas alas 1-2 cm, para luego elevarlas súbitamente a una posición normal, conducta que se repite rápidamente en varias ocasiones. Cada episodio de "temblar" toma aproximadamente un segundo. Este estudio, que se llevó a cabo durante el mes de marzo de 1991 en Dominica, tuvo como objetivo estudiar la frecuencia de temblar en estas aves. La tasa de temblar resultó significativamente diferente en diversos contextos sociales. Individuos solitarios que cantaban dejaron de cantar y temblaron a razón de $1.74/\min$ to. Aves solitarias que forrajeaban temblaron a una razón de $6.8/\min$. Mientras que conespecíficos que forrajeaban o viajaban juntos a dos metros de distancia el uno del otro temblaron a razón promedio de $28.6/\min$; aves envueltas en persecuciones, a < 0.5 m de distancia una de la otra, temblaron a una proporción promedio de $50/\min$. Individuos solitarios (n = 31) mostraron una proporción de temblar significativamente menor que la de aves sociales (dos tembladores presentes, n

= 13, P < 0.001, Prueba U Mann-Whitney, U = 43). La mayor frecuencia de temblar, en un contexto social, apoya la hipótesis de que el temblar es un signo visual intraespecífico. Esta interpretación toma peso por la ausencia de una nota de contacto en la especies y por datos que muestran que el ave siempre tiembla inmediatamente al posarse en una percha nueva.

The Brown Trembler (Cinclocerthia ruficauda), one of the endemic Mimidae of the Lesser Antilles, has a conspicuous and frequent habit of trembling its wings, the behavior for which it is named. Trembling consists of a perched bird drooping both wings 1–2 cm, then quickly raising them back to a "normal" position several times in rapid succession. Wings are not raised from the body. Both males and females tremble, and each "tremble" lasts about 1 s. Speculations about the function of trembling behavior have included: a camouflage movement making the bird resemble a bunch of dry leaves (Noble 1916), a "warning" (Noble 1916), a behavior making the bird more conspicuous (Bond 1928), and social signal with aggressive content (Zusi 1969). The purpose of this investigation was to assess the function of trembling behavior in the Brown Trembler.

After 7 d of qualitative observations of Brown Tremblers, we quantified and analyzed the frequency of trembling in various social contexts. We observed Brown Tremblers and timed trembling in 44 observation periods ranging from 2 s to 6 min in duration. Observations and measurements occurred over 4 d in March 1991, at six study sites within 1.5 km of Springfield Plantation (380 m elevation), Dominica, West Indies. Each observation period was classified into one of four categories: bird solitary (no other Brown Trembler visible to observer) and singing; bird solitary and not singing (foraging, resting or travelling); two Brown Tremblers foraging or travelling together within 2 m of each other; and two Brown Tremblers in a rapid chase, < 0.5 m apart. Mean frequencies of trembling were as follows: solitary, singing Brown Tremblers stopped singing and trembled at a mean rate of 1.74/min (eight trembles, four observation periods). Solitary Brown Tremblers that were foraging trembled at a mean rate of 6.8/min (115 trembles, 27 observation periods). Brown Tremblers foraging or travelling within 2 m of a conspecific trembled at a mean rate of 28.6/min (52 trembles, 11 observation periods), and Brown Tremblers involved in a rapid chase, < 0.5 m apart, trembled at a mean rate of 50.0/min (11 trembles, two observation periods). These differences among contexts were significant (P < 0.001, Kruskal-Wallis Analysis of Variance, H = 64.3) if all contexts are used in the analysis. Times between successive trembles, however, may not be independent within an observation period. If only mean trembling rates of social vs. solitary birds are analyzed, solitary birds (n = 31) show a significantly slower rate of trembling than social birds (two Brown Tremblers present, n = 13, P <0.001, Mann-Whitney *U*-test, U = 43).

In addition, trembling was strongly associated with changes of perch in all contexts. Among 106 perch changes observed, we noted trembling within 1 s of landing on a new perch 104 times, with only two instances of a Brown Trembler landing on a new perch without trembling.

These results, showing a faster rate of trembling associated with social contexts, support the hypothesis that trembling is used for intraspecific communication (Zusi 1969). More specifically, we suggest that trembling may function as a visual intra-specific contact signal, analogous to contact notes vocalized by many species that forage in flocks. Our observations of trembling after arrival on a new perch support this interpretation, as does the absence of a contact note used by Brown Tremblers (Storer 1989).

Trembling appears to differ both in form and function from wing-flashing observed in other Mimidae, in which wings are raised up from the body, and in which the wing-flashing behavior is associated with foraging behavior (Hailman 1960) or with the presence of predators (Horwich 1965, Michael 1970). Trembling occurred during foraging and non-foraging activity; significant variation in its rate of occurrence was related to social context, not to foraging or to the presence of predators.

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