THE AGONISTIC BEHAVIOR OF VARIED THRUSHES (IXOREUS NAEVIUS) IN WINTER ASSEMBLAGES

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This paper reports intra- and interspecific agonistic behavior of Varied Thrushes (Ixoreus naevius) concentrated at an artificially maintained feeding area following a heavy snowfall in the Willamette Valley of western Oregon. The 43.2-cm snow which fell in Benton County on 25 January 1969 and persisted as an unbroken blanket until 8 February was a 33-year record, and forced aggregations of many bird species into regions providing food and shelter. Similar congregations of thrushes in favorable areas under extended severe weather conditions are well documented (Bent 1949; Williams 1949; Ransom 1950; Gullion 1951; and Hager 1960), yet only fragmentary observations of behavior (Law 1921; Bent 1949) and interactions have been reported.

METHODS

Observations were made of Varied Thrush behavior for 22 hr, dispersed evenly throughout the bird-day, 25 January-7 February 1969. Additional time was spent recording vocalizations and photographing displays. The birds were viewed from a house window at distances of 3-9 m with the aid of 7×35 binoculars; the window was slightly opened to facilitate hearing vocalizations. Written descriptions of display sequences were made immediately following termination of action series. Photographs were obtained with a 35mm still camera equipped with a 12× lens. Vocalizations were recorded with a Uher 4000 Report-L tape recorder and analyzed with a Kay sound spectrograph, Model 6061A.

Approximately 45-50 Varied Thrushes utilized the feeder, with as many as 17 feeding simultaneously; 25 individuals were captured and banded with U.S. Fish and Wildlife Service bands and some were dyed for individual recognition. The birds concentrated their activities in an area comprised of lawns and gardens interspersed with fruit trees and scattered thickets of laurel and holly which provided shelter. Directly over the ground feeding area rose a 20-m tall Big-leaf Maple (Acer macrophylum) where birds frequently perched when not feeding.

VOCALIZATIONS

Three different call notes accompanied Varied Thrush displays during aggressive encounters. On two occasions a fourth note form was used as a thrush performed "disturbance" movements after being supplanted by a larger species. No female notes were heard.

Sound spectrograms of the first three notes are reproduced in figure 1. A clear trilled *vreee* note of 0.3–0.4-sec duration (fig. 1A) was the most common vocalization. The spacing of the pulses (0.05 sec each) lent a thrill-like quality to the note; pitch and volume were essentially constant throughout the vocalization.

The second most commonly emitted sound (fig. 1B) was a harsh *churrr*, about 0.4 sec long. A fast series of about 21 identical repetitive pulses gave a vibrant property to this note. Compared with the *vreee* sound, the overall pitch of the *churrr* note seemed lower and appeared to carry over longer distances, with a more "emphatic" quality.

The third Varied Thrush vocalization (fig. 1C) was similar to the *vreee* note in frequency, amplitude, and duration, but lacked the pulsations of the vreee. A pure ringing 0.3-0.4-sec whistle resulted. Under field conditions it was sometimes difficult to distinguish between this Ringing note and the *vreee* sound. Further, the two seemed to be used interchangeably in similar display circumstances. Careful auditory monitoring and spectrographic analysis of a sample tape-recorded series of these notes indicated that the Ringing note was emitted much less frequently than the vreee vocalization. Because I was sometimes uncertain as to which of these two notes had been given I have termed both sounds as the vreee in later descriptions of agonistic displays. Because of their apparent interchangeability, this merger should not affect contextual relations of vocalizations and displays.

In some displays the accompanying vocalizations were given either singly or two notes were coupled, spaced 0.6–1.3 sec apart. Figure 1C illustrates a Ringing note which preceded a *churrr* note. *Churrr* calls were sounded prior to the *vreee*-type notes in about half the double calls heard; however, there appeared to be no strict relationship between a specific display and priority of note type in a couplet.

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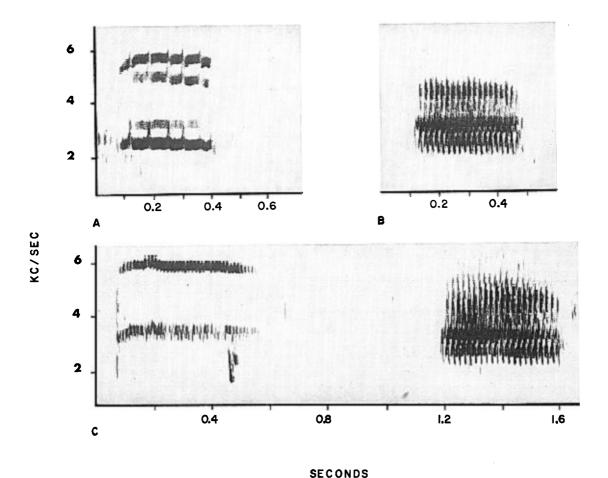


FIGURE 1. Sonagrams of notes of Varied Thrushes at Corvallis, Oregon, made with a wide band filter setting. A. *vreee*; B. *churrr*; C. Ringing note (left) and *churrr* (right). Heavy mark below Ringing note is spurious.

Under conditions of disturbance, groups of five sharp, loud *chekt* notes were given, each cluster lasting approximately 1 sec. The groups of notes were repeated at 5–7-sec intervals.

FEEDING BEHAVIOR AND INTRASPECIFIC INTERACTIONS

Each male Varied Thrush tended to feed in a restricted portion of the available food area and while at the feeder persistently defended a space 0.3–0.6 m in diameter from intrusion by other thrushes, using displays and attack. Individually recognizable males tended to return to the same feeding location following periods of perching off the area, although occasionally the specific feeding sites shifted. Certain individuals dominated others, as evidenced by their persistent aggressiveness and ability to repeatedly regain former feeding locations after an absence from the feeder. The system of fairly flexible, shifting defended

feeding areas partitioned the feeding space into a limited number of "micro-territories," each subject to only slight compression. At this feeder, where seed was dispersed in three separate patches, each approximately 1 m in diameter, space was available for about 8-10 thrushes to feed simultaneously with a minimum of "boundary patrolling." When more birds were present, many were simultaneously engaged in displaying or fighting, and consequently fewer birds could effectively feed. Normally each thrush fed for 8-10 min, departed, and returned 20-45 min later. In its absence other birds utilized the space, and upon its return, if unable to regain the former area, it chose an alternate region less strongly contested or waited and became opportunistic at darting into a newly vacant space. On certain occasions one or two especially aggressive males were able to fend off all other Varied Thrushes, but these individuals were unable to feed while concurrently continuing

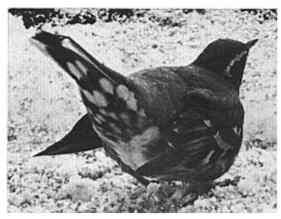


FIGURE 2. Displays of Varied Thrushes: Tail Up display as viewed by an intruding individual, showing conspicuous patterning on tail undersurface.

aggressive tactics over extended periods. Eventually the feeding area became allotted to a number of birds.

No more than two females were observed simultaneously at the feeder and only five were banded. Females were usually displaced by males, but in a few instances some successfully supplanted males. Intersexual encounters were relatively less frequent than male-male hostilities, since females appeared to avoid confrontation with males. No conflicts were noted between females. Females frequently fed in the narrow snow-melt zone adjacent to the house; males were observed eating only at the maintained feeding site. Apparently females tended to utilize alternative food supplies, rather than to compete directly with the more aggressive males.

Of the 1979 recorded intraspecific hostile displays and/or attacks, over 1800 involved conflicts at the feeder, while most of the remaining contests centered over perching positions in the Big-leaf Maple.

AGONISTIC DISPLAYS

A description of the normal feeding stance of Varied Thrushes provides a standard "reference" posture with which postures of displays and other movements can be compared. In the Standard posture the tail, back, neck and head were all horizontal and the wings folded to the sides with the remiges closed and positioned just above the tail. The rectrices were unspread and the legs partially extended. Body feathers were relaxed.

When a second individual approached or remained nearby, this Standard attitude was modified. The defender elevated its tail (Tail Up display) as much as 65° above the axis

of the body and depressed the wing tips slightly abducting them (fig. 2). Rectrices remained unspread. Frequently the undersurface of the lifted tail was oriented toward the encroaching bird, conspicuously exhibiting the normally concealed alternate pattern of white tear-shaped markings and dark patches formed by the under tail coverts. These coverts and the feathers of the flanks were loosely fluffed. Churry or vreee notes. alone or coupled, accompanied the display. When other thrushes were near, a male commonly maintained the Tail Up attitude 4-5 min as it continued to feed, periodically extending its neck momentarily (as in fig. 2) and calling vreee. An almost identical display was usually adopted after a male successfully drove off another thrush, as it either faced toward or whirled away from the fleeing individual and raised its tail to about 60°, emitting a *vreee*. In this situation the rectrices were usually well fanned and the tail was sometimes held elevated for as long as 15 sec. Frequently a bird feeding in the Standard posture suddenly assumed the Tail Up pose and ran rapidly forward 30-40 cm with neck extended and head, neck, and back horizontal as it trilled the *vreee*. Very short rapid strutting or prancing steps were taken during this short run, rather than the hopping locomotion normally employed by this species.

Another commonly performed agonistic posture, the Head Forward display, occurred at close quarters when two antagonists approached and faced one another, separated by bill distances of 2-30 cm, or when a bird suddenly alighted close to a feeding individual who immediately assumed the display. The Head Forward display formed a graded series, usually beginning as a low intensity variation of the Standard pose and terminating in a posture intermediate between the lowest and highest intensity of the display. High intensity, as used here, refers to those displays in which the angle of wing tip abduction is relatively large with respect to the Standard posture. Lesser intensities have correspondingly lesser degrees of abduction (see Willis 1967:17).

Figures 3, 4, 5 and 6 depict, respectively, low, intermediate, and two high intensity poses of the Head Forward display. Although many variations in form were observed, and a continuum of intensities was possible, the illustrated examples are typical of the overall range. In the mildest form, the body was tilted on flexed legs so that the abdomen almost touched the snow, and the tail, in line with the body axis, was sometimes partly fanned.

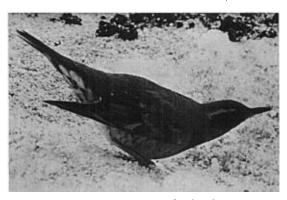


FIGURE 3. Displays of Varied Thrushes: low intensity Head Forward posture.

The head was extended and often the beak was gaped for 4 or 5 sec. Vreee notes were commonly emitted. Often both contestants engaged in this stance simultaneously, maintaining it for as long as 20 sec. Sometimes one bird performed the low intensity posture while the other held a stance of higher expression, as illustrated in figure 4. Frequently a subordinate bird fled or backed away, or a dominant bird attacked directly from a low intensity pose. In other instances one or both assumed an intermediate stance, showing greater abduction and an arched or hunched rump, and usually a depressed, spread tail. Vreee vocalizations, given as often as every 3 or 4 sec, accompanied the display. The attitude was rigidly maintained for as long as 20-30 sec, frequently terminating in attack or

Few hostile encounters progressed as far as the most intense expressions of the Head Forward display (figs. 5, 6) in which the wings were thrust out and held stiffly perpendicular to the body; occasionally the tips were abducted as much as 120° from rest position.

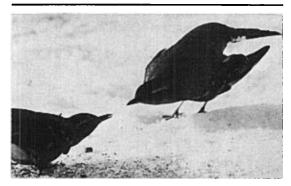


FIGURE 4. Displays of Varied Thrushes: the bird on the right is displaying with an intermediate expression of the Head Forward pose while the individual on the left shows a lower intensity stance.

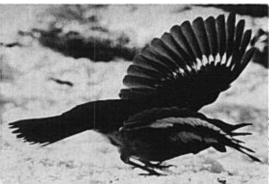


FIGURE 5. Displays of Varied Thrushes: lateral view of a high intensity Head Forward display accompanied by a *creee* call.

The remiges were parted and tipped dorsoposteriorly, conspicuously displaying the striking orange-buff band on each wing. The anterior edge of the wing was either pressed against the snow or the outstretched wings were somewhat elevated, as in figure 5. Tail configurations varied, but usually rectrices were strongly spread, the tail was elevated, and the body was tipped forward. Neck and head were held upward to the horizontal and either churrr or vreee calls were expressed about every 2 sec. When not calling, the beak was usually gaped and directed toward the opponent. These more extreme displays arose either from low or middle intensity postures or directly from the Standard feeding pose when an adversary suddenly alighted close by. Normally in the latter situations the display was maintained for only 1-2 sec before the invader fled or the displaying bird attacked. But when two birds actually faced-off, the display was prolonged, firmly held as the



FIGURE 6. Displays of Varied Thrushes: high intensity Head Forward display as viewed from the front. The bird in the foreground holds a posture of slightly less than high intensity.

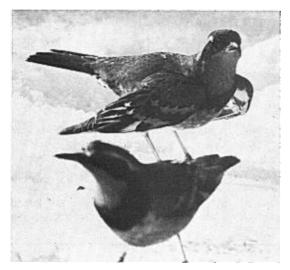


FIGURE 7. Displays of Varied Thrushes: the Quivering display.

two contestants peered at one another for up to 25 sec, before one bird fled or an attack commenced.

Both individuals did not always assume equal emphasis in their Head Forward displays (figs. 4, 6). At all intensities, feathers were neither noticeably fluffed nor sleeked. In the instant before an attack a posture similar to the Standard position was assumed.

Another intraspecific agonistic display was observed on only three occasions. This was performed only by subordinate individuals prior to an attack by another Varied Thrush, with the displaying bird always more than 40-50 cm from the opponent. Figure 7 illustrates this stance, in which conspicuous abduction and depression of the wings at both bend and tip were coupled with rapid wing quivering. Although the distal regions quivered most rapidly and showed the greatest vertical movement, vibration at the bend of the wings was still conspicuous. Abduction of wings was greater in this Quivering display than in the Tail Up or the low and intermediate intensities of Head Forward displays; in one Quivering display, wings were extended at almost right angles to the body. Both the back and the unfanned tail were horizontal. but the head was raised and maintained in an alert position throughout the quivering, with closed, horizontally-held bill. Vocalizations were not produced. Legs were extended more than in other displays. The Quivering display was the only posture in which the conspicuous black breast band of the male was prominently exposed. In the three observations of the Quivering display its duration ranged from

8 to about 25 sec and it was terminated by an attack from a second non-displaying thrush.

Actual attack postures showed little variation: head, neck, back, and tail were horizontal, the neck stretched forward, the rectrices unspread, and the wings close to the sides. Usually the beak was gaped. Locomotion was through extremely rapid hops. If attacks covered more than 2 m, a short flight added momentum. Attacked birds usually fled, but when they delayed, the attacker often delivered one or two hard pecks on the neck or breast. As the subordinate bird escaped, the aggressor usually briefly tilted his head and beak 40-45° upward and called a doublet of vreee and churrr notes, in either order. Regardless of the vocalization form, a Tail Up display immediately ensued.

Occasionally an attacked thrush offered resistance, confronting the driving bird head on; a fight invariably followed. Fighting also resulted when neither individual retreated from Head Forward encounters. Fights were brief (2–6 sec) and involved rapidly fluttering wings as one opponent locked its beak to the other's, and the two drove back and forth with twisting, side-to-side head movements. Sometimes a series of vigorous pecks occurred when bills were not interlocked. Most fighting was confined to the ground, yet some birds fluttered upward 20-30 cm before parting. No vocalizations were heard during fights. A vreee was usually trilled by the victor as it performed a Tail Up display following the fight, facing either toward or away from the departing bird.

INTERSPECIFIC BEHAVIOR

Table 1 relates the outcome of 567 observed encounters between Varied Thrushes and other species. The Varied Thrush was the most antagonistic species at the feeding area in its interactions with a majority of other species. Only three species, the California Quail, Scrub Jay, and Robin, consistently dominated Varied Thrushes. Of particular note was the aggressiveness of Robins toward thrushes. Robins were present sporadically and in low numbers (from one to three simultaneously), but every individual was overtly and persistently aggressive toward the Varied Thrushes, supplanting any that approached within a meter, and occasionally driving toward one from as far away as 2.5 m. Single Robins repeatedly attacked one thrush after another in spurts lasting 4–5 min, then paused to feed for a few minutes before resuming the drives. Male and female Robins were equally aggressive toward the

TABLE 1. Interspecific interactions* involving Varied Thrushes.

	Initiated by			
	Varied Thrush		Other Species	
	Thrush			
	Won	Lost	Won	Lost
California Quail (Lophortyx californicus)	2	2	0	4
Red-shafted Flicker (Colaptes cafer)	0	0	0	1
Scrub Jay (Aphelocoma coerulescens)	1	0	0	7
Robin (Turdus migratorius)	6	3	0	312
Starling (Sturnus vulgaris)	1	0	0	0
House Sparrow (Passer domesticus)	8	0	0	0
Redwinged Blackbird 9 (Agelaius phoeniceus)	52	0	0	4
Brewer's Blackbird (Euphagus cyanocephalus)	11	3	0	4
Brown-headed Cowbird (Molothrus ater)	12	0	0	0
Rufous-sided Towhee (Pipilo erythrophthalmus)	26	0	0	0
Oregon Junco (Junco oreganus)	38	0	0	0
Golden-crowned Sparrow (Zonotrichia atricapilla)	48	0	0	0
Fox Sparrow (Passerella iliaca)	19	1	0	0
Song Sparrow (Melospiza melodia)	2	0	0	0

^a To prevent scoring questionable events where an individual may have fortuitously changed location rather than moved in response to another bird's approach, only observed instances of interspecific displays, pecks, and overt attacks are tabulated.

thrushes, yet both were essentially indifferent to all other species. On three occasions a male Varied Thrush approached and initiated a face-off with a Robin, or attacked, but was forced into retreat by the Robin. The six instances where Varied Thrushes were successful in dominating Robins occurred during a steady rain. At this feeder, Robins appeared to suffer more from prolonged exposure to rain than did other species; they appeared wetted and were continually hunching while fluffing their feathers. Under these circumstances Robins were not aggressive toward thrushes, backing away or flying when a thrush drove at them.

In its encounters with quail, jays, Robins, female Redwinged Blackbirds, Brewer's Blackbirds, and Fox Sparrows, the Varied Thrush frequently assumed various expressions of the Head Forward display or the Tail Up display, occasionally calling *vreee* notes. Thrushes

normally reacted to the presence of Scrub Jays by simply moving away, but in one instance when a jay alighted 3 m from a thrush, the latter turned away from the jay and commenced a Tail Up display. Until the jay's departure 40 sec later, the thrush emitted five or six series of five harsh chekt notes. A similar series of notes accompanying the Tail Up display (the tail oriented toward the other bird) was given twice after a Robin approached to within 2 m of a thrush. On another occasion a Varied Thrush suddenly took flight and swooped 2.5 m directly at a feeding Scrub Jay, colliding with such impact that the thrush flipped over the jay's back. After retreating 3 m the thrush slowly flicked its tail up and down for about 15 sec before approaching to about 50 cm from the jay. There it assumed a Tail Up display and darted back and forth calling *vreees*.

The thrushes in the genera Catharus and Hylocichla studied by Dilger (1956) rarely exhibited the Horizontal Stretch counterpart of the Head Forward posture in interspecific encounters. Indeed, he noted very few interspecific displays of any type among wild, free-living birds, but found these displays were more common in captivity where unnaturally high competition existed for space, food, and water. The concentration of birds at a localized food source in the present study probably corresponds to Dilger's captive situations, thus accounting for the high incidence of interspecific display by Varied Thrushes. Undoubtedly the frequency of interactions between these species is reduced during the breeding season when they are dispersed over wide areas. In spite of frequent recourse to displays by Varied Thrushes during encounters with the above species, only Robins and female redwings responded with display attitudes, and then only occasionally. When Varied Thrushes supplanted the other species listed in table 1, displays were infrequent, and usually attacks or pecking were initiated directly from the Standard posture. In general, thrushes supplanted smaller species and were dominated by larger birds. However, sizes and weights of Robins and Varied Thrushes captured at the feeder were approximately equal.

DISCUSSION

The three agonistic displays described above probably do not comprise the entire agonistic repertoire of the Varied Thrush, for the condensation of observations into nine days in mid-winter precludes observation of hostile

displays which might be confined to other periods of the annual cycle. In a comparison of seasonal occurrence of behavior in three blackbird species, Orians and Christman (1968) found that only three of nine hostile displays are used throughout the year by Redwinged and Yellow-headed Blackbirds (Xanthocephalus xanthocephalus), and only three of five by Tricolored Blackbirds (Agelaius tricolor). My current unpublished investigations of Bobolink (Dolichonyx oryzivorus) behavior show a similar reduction in the number of forms of hostile attitudes given during the post-breeding season. Furthermore, for some species the frequencies of specific displays are subject to seasonal changes (cf. Stokes 1962). Thus, the Quivering display, observed in only three instances during this study, might in fact be a commonly performed behavior at other times.

Of these three displays, the functional contexts of only two, the Tail Up and Head Forward postures, are readily apparent. Tail Up attitudes were generally assumed by individuals presented with only a mild threat of intrusion by nearby birds, and served a spacing-out and warning function. Commonly three or four birds fed compatibly, each in its small territory, all maintaining a Tail Up pose for as long as 5 min while occasionally calling. Orientation of the patterned undertail coverts toward adjacent birds probably accentuated the warning. Usually intruding birds ceased approaching and maintained or increased their distance from an individual performing a Tail Up. Elevation of the tail does not appear to be a common behavior among North American thrushes. Dilger (1956:335) described the tail movements of the Hermit Thrush (Catharus guttatus), which at high intensity are accompanied by erection of the belly and flank feathers, as in the Varied Thrush. But the Hermit Thrush performs its Tail Raising display silently, without wing tip depression and without an orientation toward a potential opponent; also, the duration of its tail elevation is short.

When a bird persistently challenged another by approaching closely despite repeated Tail Up displays, the Head Forward attitude was resorted to by the defender. In about 30 per cent of its occurrences this display ultimately led to an attack, while in a majority of the remainder, the subordinate individual retreated or fled, either before or as the dominant bird ceased displaying in preparation to drive toward it. In all instances where both individuals took a Head Forward stance, the

bird showing the highest intensity was the ultimate victor. The most prolonged face-offs coincided with boundary disputes of two birds along contiguous territorial perimeters. Like the Horizontal Stretch given by Catharus species (Dilger 1956:342), the Head Forward signals a relatively high motivational level, predictable in the context where two adversaries meet at close quarters. Dilger (op. cit.) also described an apparently related display of the Wood Thrush (Hylocichla mustelina), the Horizontal Fluff, which differs from the Head Forward of the Varied Thrush in its striking fluffing of the breast, flank and back feathers.

The function of the Quivering display remains speculative. The situation in which it was performed suggests that the display is submissive in nature, yet it contrasts markedly in form and outcome from accepted views of submissive behavior, for submission involves neck withdrawal, leg flexion with a crouching pose, conspicuous feather fluffing, and has evolved to reduce or prevent the release of attack tendencies of an opponent. Dilger (1956:322) described the "Withdrawn Display" of Catharus species, in which wings were abducted "and rapidly shivered" as in the Quivering display, but where head and neck were tightly hunched between the shoulders. He felt that this display was given when the balance of the escape-attack tendencies had swung toward a high escape motivation. On the other hand, since the Quivering display contains elements characteristic of intimidation (extended legs, head up, extended neck) it may in fact be aggressive behavior by an intruding bird designed to "frighten" the defender (Moynihan 1955), thereby delaying or reducing the force of any ensuing attack. Or, according to the "cybernetic" view of agonistic behavior (Willis 1968), such a posture by a subordinate individual might actually accelerate escape, depending upon the outcome of past interactions between the two birds. Extended observation will be required to assess the full nature of the Quivering display's signal function.

SUMMARY

In 9 days of observations of over 1900 agonistic encounters and displays of about 50 Varied Thrushes congregated at a feeding station in western Oregon following a heavy snowfall, three display types were noted. The Tail Up display functioned to maintain distance between individuals, while the Head Forward stance occurred when two thrushes were

facing one another at close quarters. The latter display frequently prompted a retreat by subordinate birds, but if resistance were prolonged, the dominant individual attacked. Another posture, the Quivering display, was observed on only three occasions and possibly served a submissive function.

Four vocalizations were noted; three, the *vreee*, *churrr*, and Ringing note, consistently coincided with and reinforced agonistic displays, while a *chekt* was associated with disturbance conditions.

Varied Thrushes frequently interacted with other species at the feeder, persistently dominating all but three species. Thrushes initiated most of the interspecific encounters except those with Robins, and commonly assumed Tail Up and Head Forward displays in interspecies confrontations. Few displays were given by other species during these encounters.

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