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HOSTILE BEHAVIOR AND REPRODUCTIVE ISOLATING MECHANISMS IN THE AVIAN GENERA *CATHARUS* AND *HYLOCICHLA*

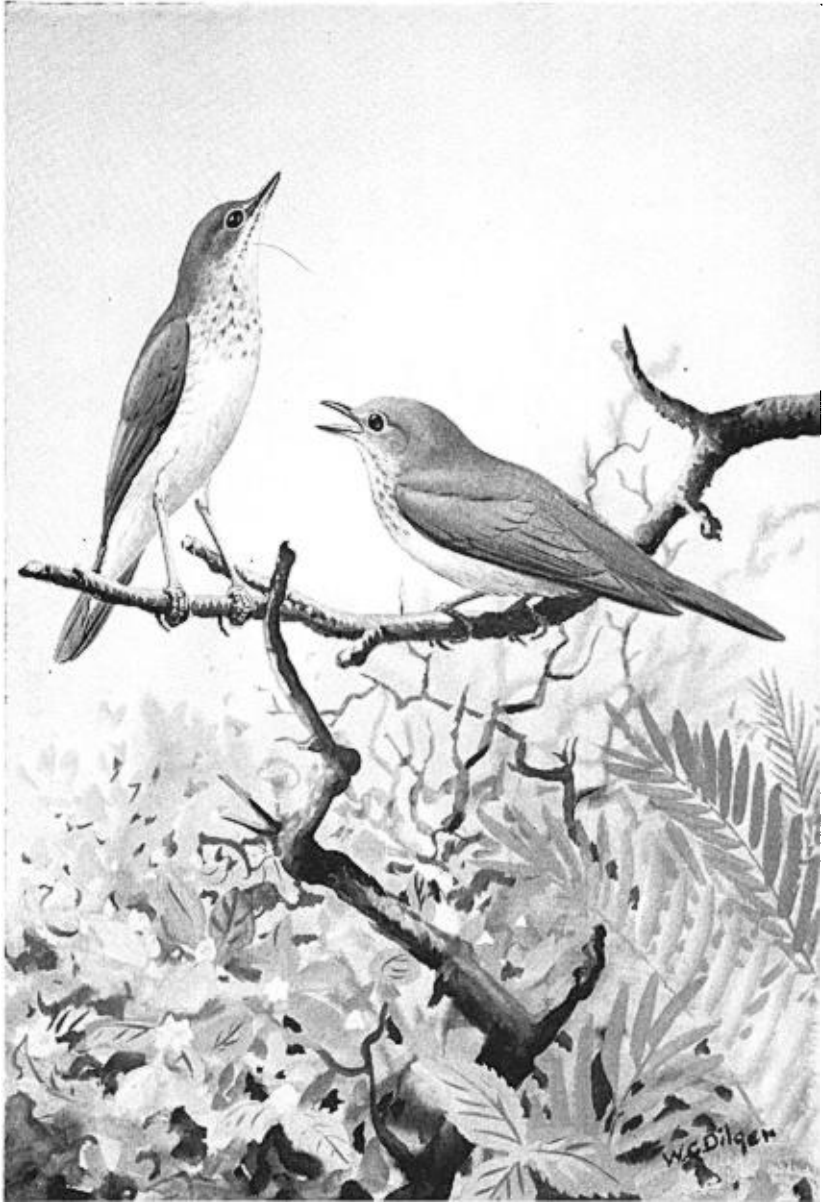
BY WILLIAM C. DILGER

ON the basis of recent anatomical, behavioral, and serological investigations, I feel that the genus *Hylocichla* of the A.O.U. checklists should be considered congeneric with *Catharus* except for the *Turdus*-like Wood Thrush, which has been left in *Hylocichla* pending further investigation (Dilger, 1956).

The North American species of *Catharus* (the Veery, *fuscescens*; Hermit Thrush, *guttatus*; Olive-backed Thrush, *ustulatus*; and Gray-cheeked Thrush, *minimus*) and the Wood Thrush, *Hylocichla mustelina* have a roughly allopatric distribution across the continent (Figure 1). There is much broad overlapping of ranges, and in montane areas of the eastern United States as many as four species (*H. mustelina*, *C. fuscescens*, *C. guttatus*, and *C. ustulatus*) may be sympatric. The four *Catharus* species are very closely related; judging by their behavior, anatomy, and serology; and all five are similar in appearance. All are forest or forest-edge inhabitants. They either do not hybridize or do so very rarely as no hybrids have been reported.

While these forms were differentiating in isolation, they must have developed differences which reduced the probability of interbreeding upon subsequent contact. Whatever these differences were they probably became greater through selection upon subsequent species contacts until they achieved the level of perfection which we observe today.

It is not hybridization that is necessarily selected against, but, rather, the formation of mixed pairs. These will be selected against since they are biologically disadvantageous. If the production of offspring is impossible, both birds will have "wasted" their time, and, in effect, two potentially productive pairs will have been wasted; the mixed pair and the birds they would have mated with if a correct



A HOSTILE ENCOUNTER BETWEEN TWO VEERIES (*Catharus fuscescens*). The bird on the left is in an Upward display and the other is in a Horizontal Stretch display; the latter is the more aggressive.

choice had been made. If hybrids are produced they are likely to demonstrate a lack of, or reduced, viability and/or poor adaptation to any available niche. Any one or combination of these possibilities would certainly supply selective pressures tending to encourage any differences between the forms which would act as species-specific recognition signals and their receptors. It is clear that mechanisms must exist which obviate or minimize the danger of mixed pairs being formed.

The comparative behavior of the species of the duck genus *Anas* has been extensively studied by Lorenz (1951). This genus, contains many sympatric, closely related species. Sibley (MS) has suggested that the females select males of their own species with which to pair. The females are all very similar in plumage pattern and color, but the males demonstrate great diversity in these features. Highly specific plumage features, coupled with highly specific movements, provide the species with signal characters to which the females respond. Spieth (1952) studied the mating behavior of various species of *Drosophila* and found the mating behavioral patterns of the males highly species specific. It must be borne in mind that not only are the male signal characters highly specific but that the female inborn "receptors" to these signals are also highly specific. Selection must operate on both the male signal characters and on the female "receptors" or releasing mechanisms.

DEFINITIONS

Before a discussion of the comparative hostile behavior of these forms can be undertaken a number of terms as used herein need to be defined.

Displacement activity.—An activity belonging to the executive motor patterns of an instinct other than the instinct(s) activated (Tinbergen, 1952). These activities are supposedly prompted by a thwarted drive or conflict between two incompatible drives. To be certain one is observing displacement activities one must have more accurate information on the motivation(s) of the animal than is generally available to those who describe them, although in certain circumstances they may be fairly safely determined.

Display.—Any stereotyped presentation of stimuli, alone or in combination such as vocal and visual stimuli, which serve a signal function to other animals.

Drive.—This term is used synonymously with "motivation" and refers to the complex of internal and external states and stimuli leading to a given behavior (Thorpe, 1951). The strength of a drive

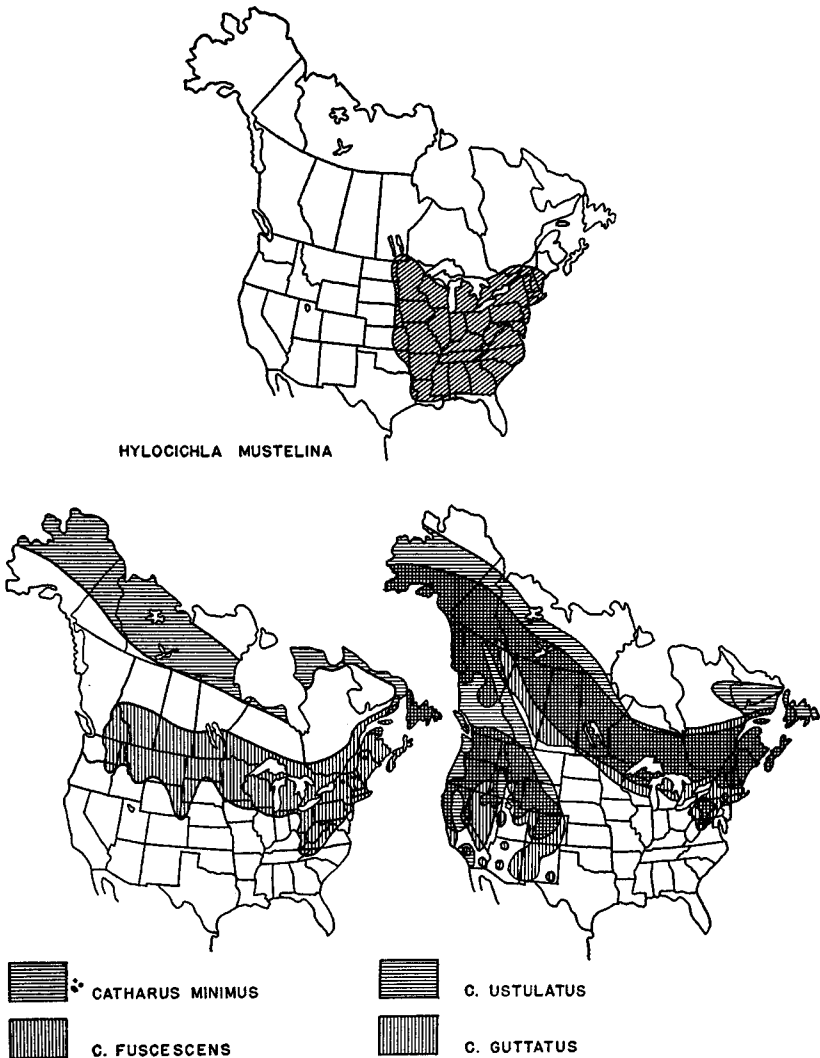


FIGURE 1. Breeding ranges of *Hylocichla mustelina* and the four *Catharus* species.

at any given instant is the sum of the strengths of the internal and external causes for that particular drive. The term "internal drive" will be used when attention must be paid to the internal causal factors and the term "external drive" will be used when attention must be paid to the external causal factors.

Habituation.—This is a type of learning associated with the waning of a response as a result of repeated stimulation that is not followed

by any kind of reinforcement. It is of a relatively enduring nature and is thus regarded as distinct from fatigue and sensory adaptation (Thorpe, 1951).

Hostile behavior.—This term refers to any behavior pattern activated by the attack and/or escape drives. This definition is used because, as far as is known, both attack and escape drives are usually, if not always, activated simultaneously (Moynihan and Hall, 1954). Often the attack and escape drives are very unequally stimulated, thus giving rise to responses in which only one or the other is overtly expressed. Sometimes both drives are overtly expressed and part of the animal will be demonstrating behavior associated with attack and part with escape (e.g., see Horizontal Fluff or Withdrawn, below). The reader is urged to read Moynihan's (1955b) excellent review of hostile behavior.

Intention movement.—These are incomplete movements caused by weak external or internal drive intensities. Because it is often possible to judge from these fragmentary or incipient movements what part of the behavior pattern is activated at the moment, or in other words what the animal may do next if the motivation rises, the term "intention movement" ("*Intentions-handlungen*") was used by Heinrich (Daanje, 1950). The term "precursory movement" may be a better one as it does not have the connotation of volition. However, I balk at introducing a new term for an already well-understood old one.

Learning.—The process that produces change in individual behavior as the result of experience. It is regarded as distinct from fatigue, sensory adaptation, maturation, and the result of surgical or other injury (Thorpe, 1951).

Releaser.—Any feature, or combination of features, in the animal's environment which stimulates a stereotyped response. It may be considered the source of the sign stimulus.

Releasing mechanism or R.M.—This is commonly expressed as the I.R.M. or innate releasing mechanism. I think, as a matter of caution, the word "innate" is best omitted or included parenthetically. This is a property of the nervous system responsible for receiving the sign stimulus and initiating the appropriate response.

Ritualization.—The process by which a behavior pattern, such as an intention movement, becomes stereotyped through selection and acquires a signal function.

Sign stimulus.—The "signal" provided by the releaser to which the R.M. responds.

HOSTILE BEHAVIOR

The discussion of the hostile behavior of these species is based on the balance of motivations concept so ably and thoroughly developed by Lorenz (e.g. 1951) and Tinbergen (e. g. 1948, 1951, 1952, 1953). There are many fine examples of work of this nature and the reader is referred, for instance, to papers by Baerends *et al.* (1955), Hinde (1952, 1953, 1955), Morris (1954), Moynihan (1955a), Moynihan and Hall (1954), and Van Iersal (1953).

The varying strengths and proportions of drives (which cause the varying pattern of displays) are deduced from observing the contexts of these displays. The extremes (in hostile behavior, for instance) are easy to identify. Strong attack or escape are obvious to anyone. The hierarchy of expression falling between these extremes may be deduced by watching many encounters between individuals and observing the circumstances in which certain behavioral patterns are seen. Often successful attempts can be made to duplicate stimulus situations experimentally (e.g. with models and recordings) and then determine whether predictable responses are forthcoming.

A comparative study of the hostile behavior patterns exhibited by *Catharus* and *Hylocichla* was undertaken in an attempt to determine the part they play in sexual and species recognition. Data on hostile behavior were obtained by watching natural encounters (in the wild and in captivity) and by observing the reactions of wild birds to models and/or recorded vocalizations played over a loudspeaker. The latter method was by far the major source of these data. The use of loudspeakers and models had the advantage of vastly increasing the number of hostile reactions seen and also provided a more nearly standardized set of stimuli by greatly reducing the variability of the external drive. Models were used instead of mounted birds as they were more durable and standardized, as well as being more readily modifiable in color and pattern.

Since most pair formation and so called "courtship" involves a mutual lessening of normal intraspecific hostile behavior, it was postulated that hostile behavior might be concerned with whatever reproductive isolating mechanisms these thrushes possess.

The method employed to elicit hostile reactions in the birds being studied was to play a tape recording of some characteristic hostile vocalization over one or more loudspeakers in the breeding territory. Loudspeakers were employed with or without the accompanying use of models, depending upon the type of investigation being conducted. An effort was made to standardize these stimuli in order to render the

results as nearly comparable as possible. In each trial the loudspeaker and model were placed, insofar as possible, the same distance from the nest, usually about 4 meters. Since the internal drive for any given behavior pattern varies greatly, depending on the stage of the reproductive cycle, an effort was made to find the nest and to estimate its stage of development. As many territories as could be found were utilized and each pair was given ample time to "rest" between experiments, usually several days, in order to minimize any effects of possible habituation induced by the experimental procedures. Ideally, of course, each bird should have been used but once and then abandoned for another, but this was impossible if enough observations were to be made to render the results at all meaningful.

The procedure was to locate as many territories as possible of all the species of *Catharus* and *Hylocichla* inhabiting a given area. These were experimented with in rotation. It was inevitable that the data gathered were chiefly of a qualitative rather than of a quantitative nature. The latter type of observations, permitting a more detailed analysis, will have to wait until some later date.

Advertising songs and other hostile vocalizations were taken from the Cornell Library of Natural Sounds and transferred onto reels of tape to be used in the field. Enough vocalization was placed on each reel to last about 8 minutes without rewinding (the maximum for the equipment used). The sounds chosen, other than the typical advertising songs, were those which were characteristic for each species as a reaction to human intrusion. Subsequent observation indicated that these sounds were the same as those used in intraspecific encounters. In order to have the various species-specific sounds as equal in value as possible, I first learned the hostile sound made by each species as I approached a nest containing eggs. This was done in case the hostile sounds differed in kind or in intensity at different stages of the breeding cycle. Subsequent observations indicated that the same hostile sounds were elicited by a given stimulus regardless of the stage of the breeding cycle, but the intensity varied with the stage of the breeding cycle. This was especially noticeable in the vociferous Wood Thrush. For example, this species characteristically utters low "bup bup bup" calls when disturbed at the incubation stage, but later when young are present this same call rises to the high pitched "pit pit pit" utterance.

The two small loudspeakers could be employed either singly or together although not simultaneously. There was enough wire to permit them to be placed about fifteen meters apart.

The models of all five species were molded from fine papier maché

and painted as accurately as possible. The eyes were of glass. Some of these models were left blank in which case they were of a uniform dull white color except for the dark eyes.

HOSTILE DISPLAYS OTHER THAN VOCALIZATIONS

The following is a list and descriptions of the non-vocal displays of *Catharus* and *Hylocichla* seen during the course of this investigation.

Supplanting attack.—This consists of the bird with higher relative attack motivation flying toward the other individual, which flees and is replaced on or near its perch by the attacker. This is a display common to many, if not all, species. Supplanting may be carried out by hopping, running, or sidling when both are sharing a common perch or are close together on the ground.

Gaping.—This is probably a ritualized intention movement to bite and is well developed in this group. The bill is pointed at the adversary and opened widely, exposing the bright yellow mouth lining. The gape is displayed in this manner for a second or two at a time. It is not employed unless the adversary is close (within a foot or so). Intention movements of attack such as Wing Flicking and thrusting forward with the head often accompany this display (Figures 2 and 4).

Bill Snapping.—This is most likely another ritualized intention movement to bite, but here the "bite" is complete and the resultant rather loud snap serves the signal function. Usually Bill Snapping is done very rapidly and is of short duration.

Crest Raising.—The crest is raised to varying degrees and is probably associated with the common behavior of many animals to look larger when under attack motivation (Figures 2 and 5).

Spread.—In this posture the feathers of the breast are laterally spread, the crest is raised, the scapulars, rump, and back feathers are somewhat raised, the plumage of the head is compressed laterally, and the tail is spread. The wings are drooped and may or may not be flicked, depending on the strength of motivation. The bird sits quite erect on the perch (Figure 2).

Wing Flicking.—The wings are repeatedly and rapidly flicked away from, and back to, the body. The motion is so rapid that the wings seem to travel less distance than they actually do but not appearing to be spread very much. This display seems to be a ritualized flight-intention movement.

Tail Flicking.—The tail is rapidly flicked in a vertical plane. Tail Flicking is often employed in conjunction with Wing Flicking and is also probably a ritualized flight-intention movement.

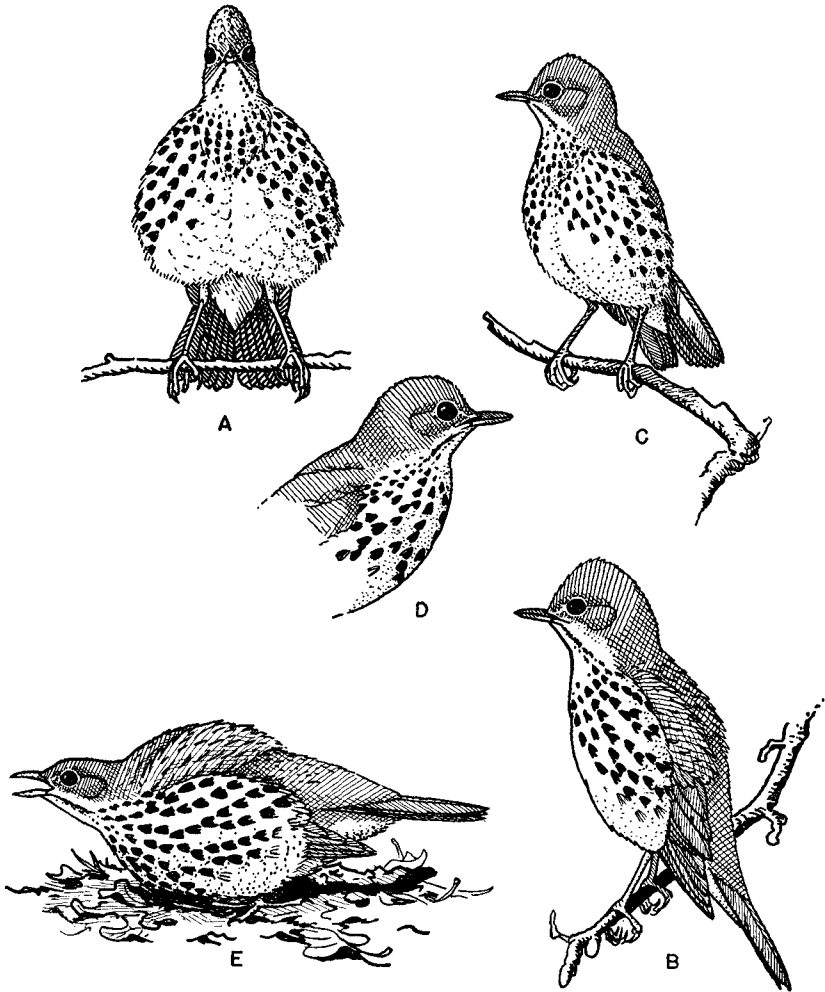


FIGURE 2. Postures of *Hylocichla mustelina*. A and B. Front and lateral views of high intensity Spread. C. Medium intensity Spread. D. Low intensity Spread (Crest Raising). E. Horizontal Fluff.

Foot Quivering.—In this display the feet are alternately and rapidly quivered against the substrate. The sound of the foot against the dry leaves of the forest floor or the papers in a cage sometimes resembles a rattlesnake's rattle. The movement is most rapid under high motivation and slower under lower motivation. Intense Foot Quivering may cause the body to quiver slightly. It seems to be a ritualized ambivalent intention movement derived from the move-

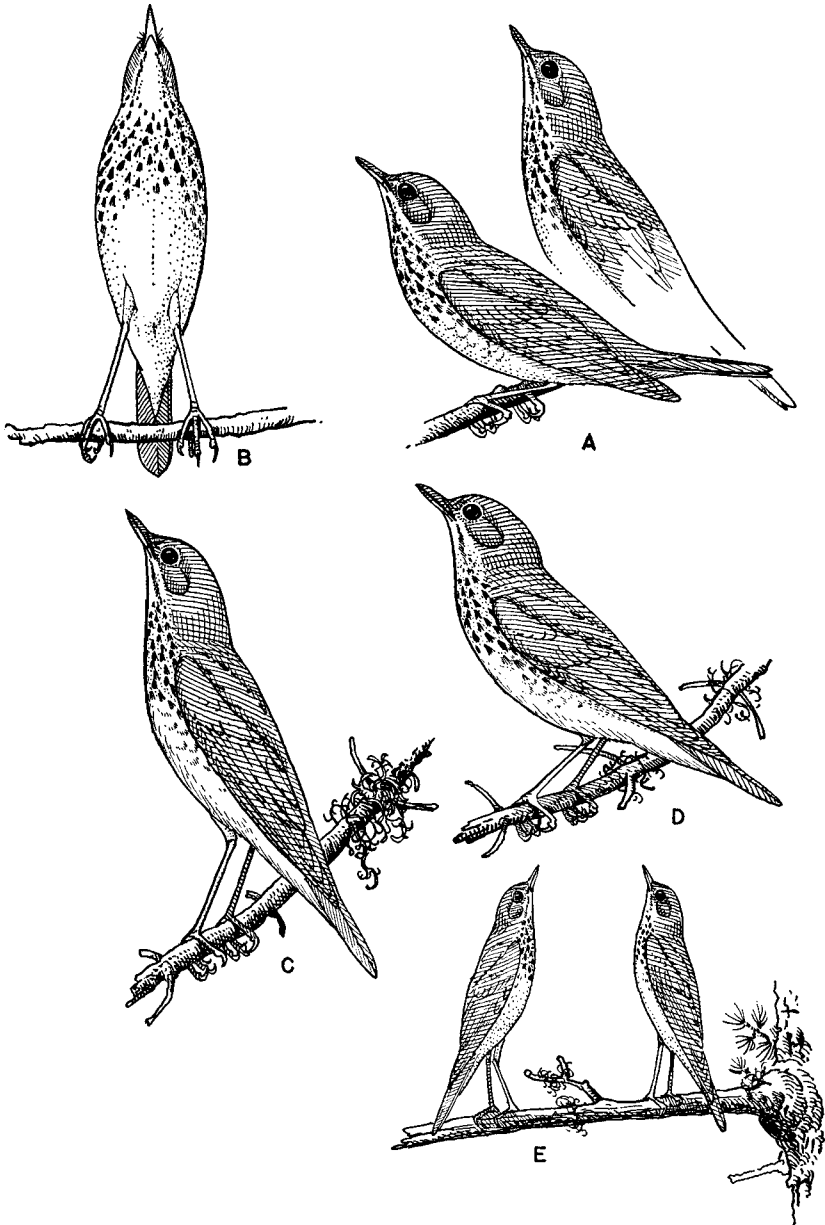


FIGURE 3. Postures of *Catharus*. A. Ordinary flight-intention movements to fly upward (shown by *C. guttatus*). B and C. Front and lateral view of high intensity Upward posture (shown by *C. minimus*). D. Medium intensity Upward posture (shown by *C. minimus*). E. Two *C. minimus* engaged in mutual display of Upwards.

ments of conflicting drives to move forward (attack) and to retreat (escape) at the same time.

Upward.—In this posture the bird stands very erect with compressed plumage and with the head and bill in line with the rest of the body (Figure 3). This attitude is assumed swiftly and retained for a second or two before the relaxation preceding the next such display, if one ensues. This has probably been derived from an intention movement to fly upward. Low intensity Upwards can be frequently confused with ordinary intention movements to fly upwards.

Horizontal Stretch.—Here the bird assumes a horizontal posture and usually has the plumage rather compressed although sometimes the scapulars and back feathers may be slightly raised. Gaping is commonly associated with this display (Figure 4). This display, always oriented toward the adversary, is probably ritualized from a posture involved in a biting attack.

Horizontal Fluff.—This posture is similar to the preceding, but the breast, scapulars, back, and flanks are greatly fluffed and the head plumage tightly compressed. Gaping is commonly associated with this posture (Figure 2).

Withdrawn.—In this posture the bird withdraws the head until it rests between the shoulders; otherwise the posture looks very much like the Horizontal Stretch. The wings are characteristically held a little way from the body and rapidly shivered (Figure 4). This posture is strongly reminiscent of the appeasement postures of soliciting females and begging young and is somewhat similar to the "freezing crouch" in response to aerial predators, which lends support to the argument that this posture is most characteristic of situations prompted by relatively high escape motivation. While in this posture the bird runs with short quick steps in a very stiff and mechanical manner.

The "freezing crouch," mentioned above, is adopted instantly upon sight of a flying predator. A suboptimal stimulus such as scaling a hat or tobacco pouch over the cage will often elicit this response. The bird quickly crouches close to the ground (or perch), the plumage is tightly compressed and the head is usually retracted between the shoulders. No movement is then made. The bird may remain in this posture for as long as two or three minutes! The eyes look particularly large as the head plumage is so tightly compressed. In captivity this response is most likely to be elicited by some subnormal stimulus if the bird is vigorously preoccupied with some other activity such as eating or a hostile encounter with a cage mate. I once watched a captive *guttatus* coming out of this posture into which it had gone because I had scaled my cap over the cage while it was engaged in attacking a mounted Button Quail (*Turnix*). He slowly straightened his legs, thus becoming higher, while the plumage was still tightly compressed. There was no other movement, not even a blink. With the plumage still compressed and still with no other move-

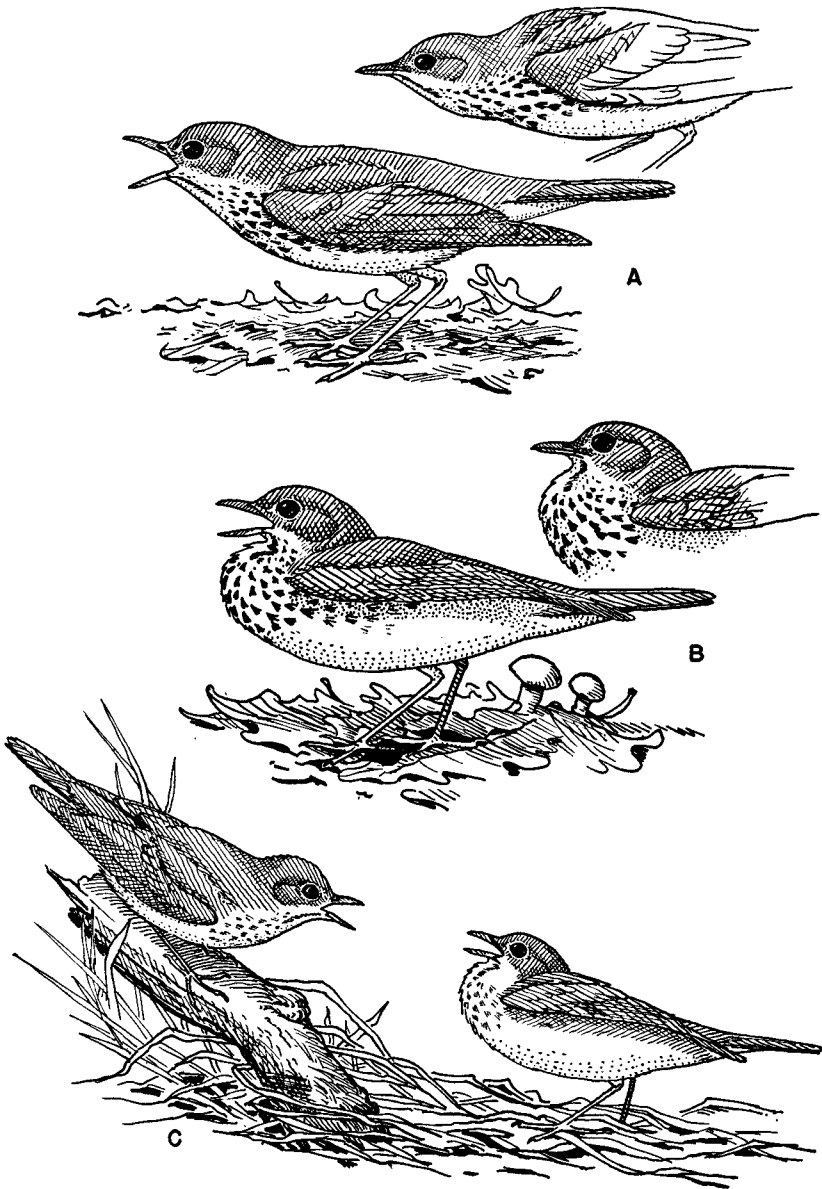


FIGURE 4. Postures of *Catharus*. A. Horizontal Stretch (shown by *C. guttatus*). The upper of the two sketches is relatively less aggressive. B. Withdrawn postures (shown by *C. guttatus*). C. Two *C. fuscescens* involved in dispute utilizing Horizontal Stretch and Withdrawn postures.

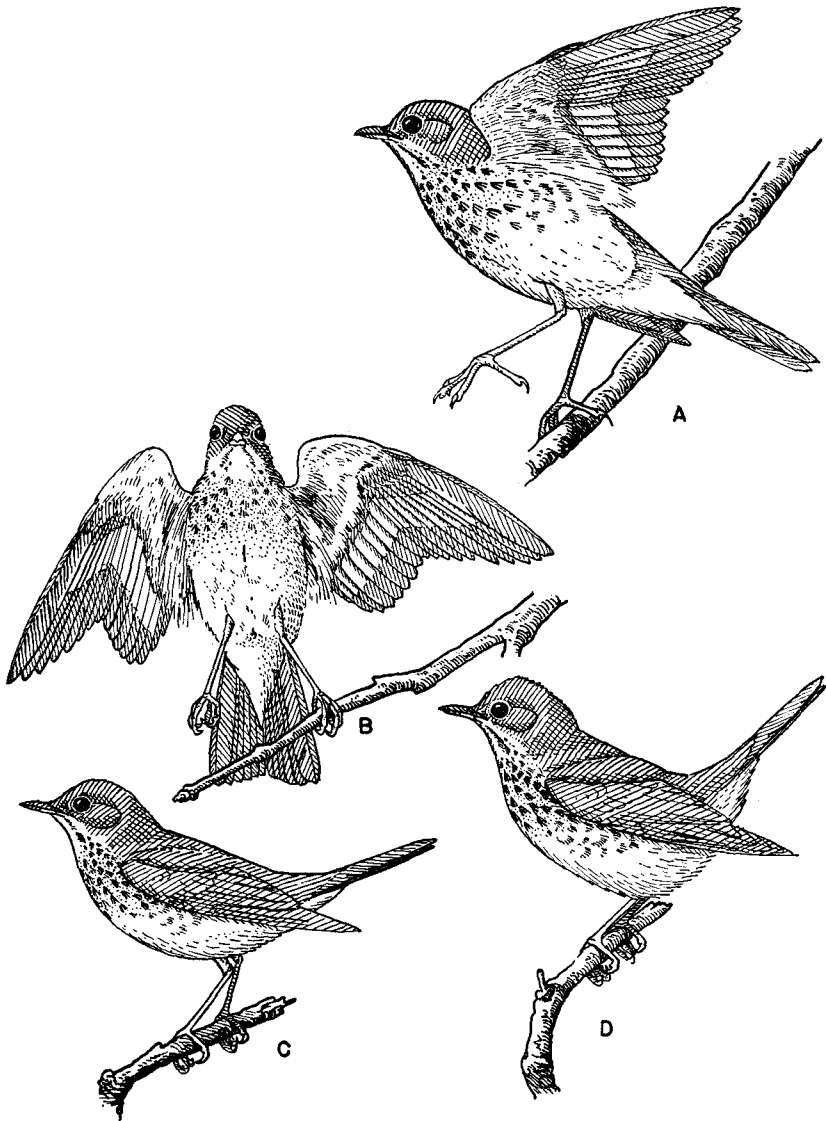


FIGURE 5. Postures of *Catharus*. A. Single Wing Flashing (shown by *C. ustulatus*). B. Double Wing Flashing (shown by *C. fuscescens*). C. Ordinary Tail Raising of *C. guttatus*. D. More aggressive Tail Raising of *C. guttatus*.

ment, an intention movement to Foot Quivering was made, soon followed by rather intense Foot Quivering as the plumage slowly relaxed. Here the thrush gave a little start as if suddenly awakened and vigorously resumed his attack upon the mounted bird.

Wing Flashing.—This display may be either double or single. In double Wing Flashing the bird, facing the opponent, stands erect and quickly flashes both wings and then typically flees. In single Wing Flashing (Figure 5) the bird is oriented at right angles to its opponent, and the wing nearest the opponent is rapidly flashed for a moment before the bird flees. The far wing in this case is kept folded. The conspicuous buffy wing stripe is prominently displayed in both types of Wing Flashing. May (1949) describes a similar display in the Willow Warbler (*Phylloscopus trochilus*). It seems likely that this display has been evolved and ritualized from a simple intention movement; perhaps a balancing or flying movement.

Tail Raising.—The tail is rather quickly raised and slowly lowered to its normal position (Figure 5). This movement may have been derived from an inhibited flight intention movement or from an "after discharge" of flight motivation (see Tinbergen, 1952). The more extreme form of this display probably is the result of greater conflict between attack and escape drives or perhaps is the result of higher intensity inhibited flight movements. During high intensity Tail Raising, the belly plumage is usually fluffed in synchronization with the upward movement of the tail and is relaxed upon the downward movement. The tail is also raised higher in these situations (Figure 5).

Winnowing.—This is a sound, apparently produced by the wings, which is always heard in conjunction with flying attacks even while the bird is calling. It is a rapid, tremulous, mellow, whistling sound.

COMPARATIVE HOSTILE BEHAVIOR

Supplanting attacks and fleeing occur if the attack or escape drives are greatly disproportionate. This is true of both interspecific and intraspecific encounters. Supplanting attacks in *Catharus* and *Hylocichla* are often without vocalization; even *mustelina*, the noisiest of the five species, is frequently silent. No other displays are associated with supplanting except for occasional Bill Snapping and perhaps advertising song or other hostile vocalizations. However, if the attacked bird does not flee, it will remain for a varying length of time while engaging in mutual hostile displays with the attacker. These displays on the part of the attacked bird may be little more than Wing Flashing or some other display associated with relatively

or actually higher escape motivation. If the attack motivation of the attacked bird is stronger, any number of other displays may ensue such as Upward, Horizontal Stretch, etc. Most of the displays noted are the result of conflict between the attack and escape drives and, as mentioned above, a great preponderance of one of these drives over the other merely elicits attack or fleeing as the case may be. This is the expected condition and is in accord with similar work done on other birds; e.g. Hinde's work on the Chaffinch, *Fringilla coelebs* (1953) and on the Great Tit, *Parus major* (1952). If the attack and escape drives are in virtual balance, then some manifestation of displacement activity, as they are believed to exist (Tinbergen, 1952), would be expected to occur in order that the animal may "resolve" its conflict. This subject is discussed more fully below.

WOOD THRUSH (*Hylocichla mustelina*).—This species is discussed separately as it differs markedly from the remaining four species in many of its hostile behavior patterns. The hostile reaction having the lowest threshold in this species is generally little more than sporadic Wing and Tail Flicking with Crest Raising (low intensity Spread) appearing as the motivational levels rise. The hostile calls associated with weak activation of the attack and escape drives are rather rapid, low "bup bup bup" sounds, which often sound like a low guttural chuckle. These low intensity reactions are released by mild stimuli such as a human or even conspecific intruder beginning to approach the territory.

Higher threshold responses are associated with an exaggerated spread of the breast plumage (giving the appearance of a large round shield thickly and heavily spotted with black). This display is accompanied by other plumage adjustments (see above) and is termed the Spread (Figure 2). Spread occurs in varying intensities depending on the strength of the external and internal causal factors. Some of the various intensities are depicted in Figure 2.

Wing and Tail Flicking are often seen in conjunction with Spread but are most evident in situations characterized by a fairly low level of both attack and escape drives. Consequently, Wing and Tail Flicking are most associated with the low intensity Spreads. Spread is typically oriented to direct the maximum area of the breast toward the opponent; whether in intraspecific or interspecific encounters. In order to "avoid" leaning too far forward or backward, the bird tends to perch nearly as possible at the same level as the adversary; especially when threatening from nearby.

The following extracts from my notes will show typical responses from this species.

May 22, 1953; Ithaca, N. Y.; 3:30 P.M.; Territory No. 1 in second growth beech-maple woodland. Incubation about 7 days. The male is delivering advertising song from a conspicuous perch within about 60 feet of me. As I moved closer, he stopped singing and raised his crest slightly. As I continued to approach he uttered low chuckled "bup bup bup" notes and slightly spread his breast feathers. Some Wing and Tail Flicking. . . . I fastened a *mustelina* model to a branch of a maple sapling about 6 meters from the nest and level with it. The female was incubating. I retired to a path about 20 meters downslope from the model and nest. The female continued to incubate. The male resumed advertising song. The male began foraging on the ground about 20 meters to my left and about an equal distance from the model. After a few minutes he flew toward the model and perched within about a meter from it. Spread was assumed instantly. The bird was silent. He hopped and fluttered from twig to twig all around the model; Spread being adopted upon each pause. One short burst of "pit pit pit" calls was made at this time. He finally perched right next to the model and delivered a light tap to it with his bill and instantly fled. From a short distance away he silently regarded the model which had fallen forward slightly by this time. He flew back to the model and resumed his hopping and fluttering about interspersed with Spreads. Suddenly he composed his plumage and jumped to the back of the model and attempted coition. The nearly horizontal position of the model may have been responsible for releasing this behavior and probably the model's passiveness contributed also. He fluttered on the model's back for a few seconds, his feet slipping repeatedly on either side of the model's shoulders as his bill attempted to grasp a non-existent crest. He suddenly flew to the ground and apparently foraged for a moment and then flew back and repeated his coition attempt without any preliminary Spread posture. This pattern of attempting coition and flying to the ground was repeated 20 times before "interest" was lost! I retrieved the model and found that the lower back and rump were slightly damp with what was apparently seminal fluid. When I appeared to take down the model he again adopted low intensity Spread and uttered loud "bup bup bup" calls which persisted until I left the vicinity. The female was still incubating.

May 22, 1954; Ithaca, N. Y.; 6:00 P.M.; Territory No. 2 in a *Sambucus* thicket area of second growth beech-maple forest. Incubation just began. James M. Hartshorne and I approached territory. Male raised crest and slightly spread breast feathers. Female on nest. We placed a speaker on either side of the nest and each about 6 meters from nest and about 2 meters from ground. A *mustelina* model was placed atop the right hand speaker. While this was going on the male uttered almost constant "bup bup bup" calls and was in perpetual low intensity Spread. We retired to about 15 meters from nest and played *mustelina* advertising song through the right hand speaker. The male instantly responded with advertising song of his own and was in high intensity Spread. He flew to about three meters from the speaker and model but seemed "afraid" to go closer. After eight minutes of this I switched to the left hand speaker without the model. The male again engaged in song duel but seemed "confused" by model in one place and vocalizations in another. After eight minutes elapsed, I switched to the right hand speaker and played "pit pit pit" calls in conjunction with model. The female instantly left nest and both "mobbed" speaker and model but did not approach closer than about three meters. Both birds adopted Spread postures and constantly uttered hostile calls; "bup bup bup" in male and "pit pit pit" in female. Female seemed more highly motivated than male. After about five minutes of this, both birds retired

out of sight and were silent. Wing and Tail Flicking seemed more intense when Spread was of low intensity and rare during high intensity Spread.

June 2, 1953; Ithaca, N. Y.; 6:00 A.M.; Territory No. 11 in small maple in second growth beech-maple woodland. Young just hatching. Robert Stein and I were recording *mustelina* vocalizations. I put my hand on edge of nest, female left silently only to return instantly with high intensity attack consisting of swooping at me (Supplanting) and uttering high pitched "pit pit pit" calls. As she passed my head, she Bill Snapped loudly and a loud winnowing sound was heard at the same time. This apparently was made by the wings. The male did not supplant but remained a little distance away and constantly uttered slightly lower pitched "pit pit pit" calls while in a medium intensity Spread. Some Wing and Tail Flicking. The female attempted to supplant me as long as I remained at nest.

The breast skin from a *mustelina*, dried with the feathers arranged in the Spread attitude was affixed to a wire and presented to territorial males. This was done upon six different occasions and on different territories each time. This arrangement was threatened in every case but never with the intensity elicited by a whole bird as represented by my models. Low intensity Spreads, and once a low "bup bup bup," call were made but this was all it elicited and then only for a short time, about two or three minutes before it was ignored. One male gave it a tentative peck and fled. It would certainly seem that the expanded breast plays an important part in the effectiveness of the Spread but that the entire bird is necessary to release a maximum response.

The hostile vocalizations, other than the advertising song, seem to be merely the "bup bup bup" sounds mentioned above given at different intensities so that they become higher pitched with increased motivation. The notes grade insensibly from these "bup bup bup" sounds to a loud, high pitched "pit pit pit" as the motivation level rises. There seems to be no special display pattern associated with higher escape motivation except for a general slimming of the plumage which is so common in many birds and may be partly an intention movement to fly. The bird simply flees when its escape drive is greatly in excess of its attack drive.

When the attack drive is greatly predominant the bird delivers an aerial attack by swooping at the adversary while uttering high intensity hostile calls and Bill Snapping. Winnowing is sometimes heard during these Supplanting attacks and seems characteristic of a relatively high intensity attack drive (see June 2 field notes above). This is most often heard when the birds have young in the nest.

Gaping has not been observed during supplanting attacks and seems to be confined to encounters between perched birds. Bill Snapping is usually confined to flying attacks. Gaping is associated

with more nearly conflict situations between attack and escape, and Bill Snapping with much higher relative attack motivation. Encounters between birds perched in close proximity often lead to Gaping by at least one of those involved. Bill Snapping is probably associated more with flying attacks because Gaping or other visual displays would necessarily be shown too briefly under such circumstances to be as effective as an audible display such as Bill Snapping.

Gaping is common in the Horizontal Fluff. This posture seems to be prompted by a rather sudden and close confrontation of a situation stimulating intense conflict between attack and escape. I have noticed what seems to be an identical posture in the American Robin (*Turdus migratorius*) in response to similar stimuli. I have not seen this display often enough in *mustelina* to feel at all sure of its motivational level. Consequently I have not included it in Figure 6 although it undoubtedly belongs along the line of increasing general motivation; probably somewhere above the middle. The head plumage is tightly compressed, which is apparently indicative of the escape component of the posture, and the enormously fluffed body plumage is indicative of the attack component of the posture. The following observation will serve as a good example of a situation prompting Horizontal Fluff.

On October 23, 1955, I threw a live earthworm into the cage (containing a Wood Thrush, an Olive-backed Thrush, and a Hermit Thrush. This latter individual was socially dominant over the Wood Thrush and usually had little difficulty in stimulating fleeing in it) and the Wood Thrush grasped it in its bill and was preoccupied with the worm when it immediately received a strong Horizontal Stretch with Gaping from the Hermit Thrush. The Wood Thrush, instead of instantly fleeing, dropped the worm and assumed the Horizontal Fluff, whereupon the Hermit Thrush fled!

Crest Raising, employed often enough without Spread to warrant separate consideration, is very much like the Tail Raising of the Hermit Thrush in action and motivation. The reddish crest feathers are quickly raised and rather slowly lowered and may serve as a species-specific recognition signal as well as having other hostile components. Like Tail Raising in *guttatus*, the crest is raised and lowered upon almost every major shift in the bird's position.

The advertising song consists of a series of flute-like phrases which are grossly similar to those of *guttatus* although louder and lacking the "tranquil" character of the latter. Bent (1949: 115) includes a rather good description of the advertising song. As mentioned above, the advertising song may be given in conjunction with the Spread display but usually not unless the adversary is in sight. I

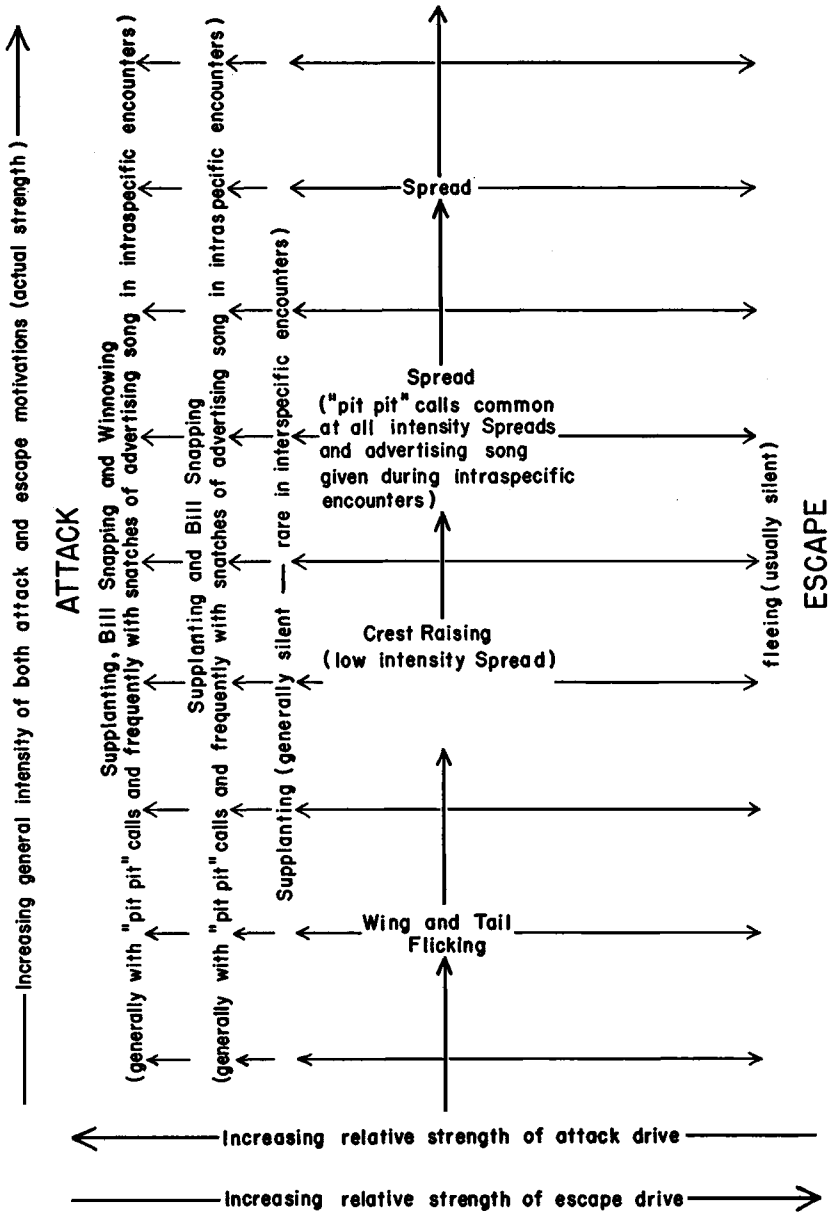


FIGURE 6. Diagram of the hostile behavior patterns of *Hylocichla mustelina*. See text for explanation.

have often watched birds engaged in song duels with my loudspeakers, gradually working closer until the model atop the speaker was sighted. At this instant the bird would adopt the Spread display and usually continue singing. Out of the 130 separate experiments with speakers and/or models that I performed on *mustelina* territories, I observed 15 instances of advertising songs preceded by a series of very high pitched, querulous notes (distinct from the "bup bup bup" calls) which gradually increased in frequency of deliverance until they graded insensibly into the song. In each of these cases the bird was hostilely motivated by a speaker and/or model. It is apparent that *mustelina* does not employ the wide variety of hostile sounds exhibited by each of the *Catharus* species nor does it have as many or as varied other hostile displays.

VEERY (*Catharus f. fuscescens*), EASTERN HERMIT THRUSH (*C. guttatus faxoni*), EASTERN OLIVE-BACKED THRUSH (*C. ustulatus swainsoni*), and BICKNELL'S GRAY-CHEEKED THRUSH (*C. minimus bicknelli*).—These four forms, with few exceptions, exhibit similar non-vocal displays. Their hostile vocalizations, however, are mainly different and will be treated separately. The chief differences among the non-vocal hostile displays employed by these species seem to involve differences in releasing threshold values. This is easy enough to see in the field but difficult to measure exactly without a great deal of quantitative study.

Low general motivation of both drives in balance is associated with Foot Quivering, a display not used by *mustelina*. Wing and Tail Flicking and slight Crest Raising are also associated with a low general motivation of both drives in balance but are not as indicative of as low a general motivation as is Foot Quivering.

Foot Quivering was first seen in a captive Veery, and some plausible explanation was sought. The one that seemed most likely at the time was thought to have something to do with food getting. It was supposed that the bird might employ these movements to flush insects from the detritus of the forest floor. This idea was consistent with what has been observed in many species of birds that use the feet in some way to help flush prey from hiding places in mud, water, or some other substrate. Tinbergen (1953) discussed this behavior in birds and refers to it as "paddling," which implies a slower type of motion. I have seen motion pictures of various wading birds foraging slowly in shallow water and stirring the bottom with one foot while watching the spot being agitated. In every case the foot motion was quite deliberate and rather

slow although this did not necessarily invalidate the possible insect-flushing function of Foot Quivering in *Catharus*.

I have looked for this behavior in the wild and have never seen it employed by a foraging bird. However it has frequently been seen in mild conflict situations (e.g., conflicts between attack and escape, feeding and sex drives). All four species have been seen engaged in this behavior in the wild, and I have seen it many times in my captive birds (*guttatus*, *ustulatus*, and *fuscescens*). It is often seen because of its low intensity nature. It is not oriented toward an opponent in any way as is Gaping, for instance.

The following two extracts from my notes are typical observations involving Foot Quivering.

May 30, 1954; Ithaca, N. Y.; 7:00 A.M.; *fuscescens* territory No. 5. Nest not found. A speaker was placed in a small sapling and I retired to about 15 meters from speaker. Before I began to play sound through the speaker, a *fuscescens* flew to the sapling containing the speaker and "investigated" it. He fluttered and hopped all around about the speaker, dancing from twig to twig and Foot Quivered incessantly. I switched on *fuscescens* advertising song, and he immediately fled to a tree about 20 meters away and began to sing. He then gradually worked his way back to the speaker, singing snatches of advertising song all the while. He began to look for his adversary, but since I did not have a model associated with the speaker he had nothing against which to orient an attack. One Upward was made in front of the speaker and about a foot from it. Except for advertising song, however, he did little except behave in a very agitated manner—flitting from perch to perch, never still for an instant. The advertising song was very faint when he was close to the speaker but much louder when he happened to be some distance away. By turning down the volume, I could lure him back, and by turning it up, I could send him away. Apparently the louder the song, the greater the amount of relative escape motivation experienced by the bird.

May 9, 1955; Ithaca, N. Y.; 5:00 P.M.; captive *guttatus* (hand raised since 5 days old). A bottle of ink was placed in the cage (strange object) and the thrush regarded it for a moment from his perch, first with one eye and then with the other. He then hopped to the floor of the cage and gradually approached, Foot Quivering all the while. He finally reached the bottle in a circuitous fashion, still Foot Quivering, and gave it a slight peck, whereupon he immediately compressed his plumage and fled only to remake his Foot Quivering approach as before. . . . Here the conflict seemed to be between approaching and investigating the bottle (attack) and fleeing from it (escape).

Gaping in *Catharus* is much the same as it is in *Hylocichla mustelina*. It was once observed employed during an Upward display assumed by a *fuscescens*. This must be rare as 27 encounters utilizing Upwards were seen involving *fuscescens* and Gaping was observed only that one time. It is most frequently seen in conjunction with the Horizontal Stretch and, to a lesser extent, the Withdrawn. The mouth linings of these species are also bright yellow. Bill Snapping,

as in *H. mustelina*, is associated with relatively higher attack motivation than is Gaping and is usually given by a bird making a supplanting attack prompted by a relatively high attack drive. These forms also employ Wing and Tail Flicking in much the same context as does *H. mustelina* (see above). Wing and Tail Flicking have never been seen in conjunction with the Upward display. The Upward display is characterized by the nearly vertical position of the bird and the extreme compression of the plumage (Figure 3). Upward has been seen only in intraspecific encounters. It is apparently indicative of a fairly high general motivational level with the attack and escape drives in close balance, with attack perhaps slightly predominant. In *minimus*, the bright yellow base of the mandible is displayed conspicuously during this posture and, interestingly enough, it is *minimus* that employs this posture most often and in which it seems to have the lowest threshold. Usually both birds involved in the hostile situation will perform Upwards in more or less unison while facing each other and generally but a few inches apart. Hartley (1949) describes a similar posture in the Mourning Chat (*Oenanthe lugens*) except that the belly and lower breast feathers were fluffed. The Upward posture in *Catharus* also seems very like the Head Up posture, both in appearance and motivation, described by Hinde (1952) for the Great Tit (*Parus major*). The Upward posture varies somewhat in appearance with varying strengths of motivation. Upwards prompted by low motivations (for Upwards) are often difficult to distinguish from the ordinary intention movement to fly up. Sometimes one Upward will prompt simple fleeing in the opponent. More often, however, both birds will perform one or more Upwards before one begins to show behavior more clearly associated with increasing relative strength of escape drive. The following, taken from my notes, will serve as characteristic examples of encounters involving Upwards.

June 10, 1953; Whiteface Mt., Essex Co., N. Y.; near summit at 9:00 A.M. While crawling on hands and knees through thick spruce and balsam cover I heard several "beer" calls (of *minimus*) close at hand. I immediately lay still and watched. Next I heard the sound of wings and at the same instant, through a small opening ahead of me, I saw one (*minimus*) land on a small branch within about four meters from me. It bill wiped as though it had just been feeding on something. All of a sudden a second (*minimus*) landed on the same perch and about a foot from the first bird which immediately assumed an Upward. The second bird also assumed an Upward a split second later; both birds subsided at the same time and the first bird gaped, from a Horizontal Stretch, at the second bird which promptly flew off without being chased by its adversary.

June 1, 1954; Ithaca, N. Y.; 10:30 A.M. in beech-maple woodland on shore of Beebe Lake. Speaker and model of *fuscescens* on rather large maple branch about two meters from ground and next to trunk. As soon as *fuscescens* advertising song

begins to play over the speaker, one (*fuscescens*) flies in and alights in front of the model which is perched atop the speaker. He immediately assumed an Upward, followed by two more. He then flew away and began to answer the speaker with advertising song.

June 5, 1954; Ithaca, N. Y.; 1:00 P.M. possible (*guttatus*) territory in beech-maple forest near margin of power line cut. A model of *guttatus* was placed in small sapling near where one was heard singing a moment before. After a few minutes the bird resumed advertising song. Soon one (*guttatus*) appeared which landed close to model and assumed an Upward. He relaxed in about two seconds and pecked at the model and fled.

June 6, 1954; Ithaca, N. Y.; 7:00 A.M. possible (*guttatus*) territory near small pond in beech-maple woodland. While sitting quietly on a fallen log, I noticed one (*guttatus*) fly to a nearby branch and begin to sing. Almost immediately a second bird flew in and landed in front of the first and both adopted Upwards simultaneously as far as I could tell. Three more Upwards were made in unison whereupon the second bird adopted a Horizontal Stretch with Gaping and the first bird did likewise but followed almost immediately with a Withdrawn, Wing Flashing (single) and fleeing. The second bird made many intention movements of attack (Wing Flicking and thrusting forward with the head) while in the Horizontal Stretch. It looked as though the first bird was an interloper on the second bird's territory.

As may be seen from the last incident taken from my notes, a rather complicated series of displays may ensue before one of the contestants actually flees. If, after an Upward or two, the less aggressive bird does not flee, it will most likely adopt the Withdrawn display (Figure 4) while its opponent adopts the Horizontal Stretch display (Figure 4). Both birds may adopt the Horizontal Stretch and a varying amount of "see-sawing" back and forth ensues. These "see-sawing" encounters probably occur because as one bird advances his attack drive gets relatively lower and the escape drive gets relatively higher, causing him to retreat. The same is true for his opponent and consequently the alternate attacking and retreating occurs. Eventually one bird will most likely adopt the Withdrawn display and, if no unexpected reversal takes place in the relative aggressiveness between the two birds, a single or double Wing Flashing will ensue before actual fleeing takes place (Figure 5). Of course, one bird may flee at any point in this series of events. Sometimes a fleeing bird is pursued by its opponent and sometimes not. Intraspecific encounters very rarely lead to a Bill Snapping supplanting attack as is usually the case with interspecific encounters. Most of the encounters involving this rather elaborate series of hostile displays are between the sexes, although they are often seen during encounters between males. The encounters between males and females lead to more nearly balanced conditions between attack and escape drives. The males are motivated to drive the females away from their territories, and the females are strongly motivated to remain. Rival males that trespass are

usually driven away with relative ease. A simple supplanting attack usually suffices although occasionally males will have enough attack motivation to remain for a varying length of time before being driven away. In these circumstances one is apt to observe more displays.

Tail Raising, employed characteristically only by *guttatus*, seems to be the only unique display among these four species. I have not seen it performed by any of the other species, but Bent (1949: 218) relates an instance where, seemingly, a *fuscescens* employed Tail Raising in conjunction with an Upward. Certainly this cannot be usual or characteristic. Ordinarily it is performed by a Hermit Thrush (both sexes) just once after every major shift in position made by the bird. The tail is raised rather quickly and lowered to the normal position quite slowly. This movement is correlated with the reddish tail of the Hermit Thrush just as the Crest Raising of the Wood Thrush is correlated with the reddish crown. The motions of display are similar in both cases; a rather quick initial movement and a slower second movement. These displays have undoubtedly evolved to ensure maximum conspicuousness; this particular combination of speeds of movement renders the displays most noticeable.

In ordinary Tail Raising, the tail is not raised much more than 30 degrees from the horizontal, and no other part of the bird is involved in this display, which seems to serve chiefly as a species-specific recognition signal. The following account, taken from my notes, suggests one of the uses of this display.

May 30, 1954; Ithaca, N. Y.; 8:00 A.M. in beech-maple woodland near beaver pond on Connecticut Hill. I was watching a (*fuscescens*) territory. The male was uttering advertising song from a perch about 3 meters from the ground and in full view. The nest hasn't been found yet. While watching him (*fuscescens*) I heard a slight scuffling in the leaves and turned to see a *guttatus* foraging along on the forest floor and coming toward the *fuscescens* which hadn't seen him yet. All at once the *fuscescens* saw the *guttatus* and made an obvious intention movement to fly down in a supplanting attack, but at this instant the *guttatus* flew upward to a small twig about a foot from the ground and Tail Raised whereupon the *fuscescens* immediately subsided, bill wiped and sat erect on the perch and began to sing once more. The *guttatus* continued to forage through the *fuscescens* territory and out of my sight.

In situations characterized by higher attack and escape motivations, however, the frequency of Tail Raising increases markedly and the tail is raised much higher than is usual. The belly plumage is fluffed as the tail is raised and becomes more compressed as the tail is lowered. This display, used only by *guttatus*, is characteristic of motivational levels of attack and escape above Foot Quivering but not as strong as those eliciting Upwards and the other displays noted. The fol-

lowing incident will provide a typical instance where this higher intensity Tail Raising is seen.

July 19, 1954; Ithaca, N. Y.; 7:30 A.M. in beech-maple woodland near beaver pond on Connecticut Hill. I placed a *guttatus* model in a small sapling near where I had heard one (*guttatus*) singing a moment before. After several minutes had elapsed, one (*guttatus*) came into view on the forest floor. He hopped from twig to twig closer and closer to the model, Tail Raising all the while. He finally perched directly in front of the model and did an Upward and flew away. He was silent the whole time.

A slight raising of the crest is sometimes noticed in conjunction with the higher intensity Tail Raising. This and the ventral fluffing may be thought of as homologous to the Spread display of *H. mustelina*. However, Crest Raising and other erections of the plumage are common among many forms of birds and no special emphasis need be placed on this display of *guttatus* as evidence for close relationships between *guttatus* and *mustelina*. Except for the common thrush hostile patterns of Gaping, with conspicuous yellow mouth lining, Bill Snapping, and Wing and Tail Flicking, *H. mustelina* and the four *Catharus* species are very different in their important hostile behavior patterns.

The four species of *Catharus* are not nearly as vocal as is *H. mustelina* although they do seem to possess a greater variety of sounds. Their hostile calls, for the most part, are not clearly the result of varying the pitch of the same utterance in response to greater force of delivery owing to higher motivation. The relatively low intensity hostile sounds are very different among the species, particularly the species most often in contact. The highest intensity hostile utterance of all, and one which has the highest threshold, is a rather high-pitched, querulous, snarling sound. This sound, with almost imperceptible differences, is common to all four species. It is uttered rarely and only under extreme attack motivation. This sound is quite similar to the nasal snarl of the Red-eyed Vireo (*Vireo olivaceus*). The species which seems to have the lowest threshold for this sound and the one which has been heard to utter it the most often is *ustulatus*. It may be that it has had its threshold lowered by the selective pressures supplied by the somewhat ecologically competing Red-eyed Vireo.

The only other hostile utterances that sound somewhat similar are the "veer" call of *fuscescens* and the "beer" call of *minimus*. These two calls are occasionally reciprocally confused by these two species (Figure 8). Since these two species are rarely sympatric, species

recognition difficulties are unlikely to arise despite the occasional confusion of these two notes.

Hostile vocalizations of the Veery (*C. fuscescens*).—The hostile calls of the Veery consist mainly of the "veer" call mentioned above, which is given in addition to advertising song in intraspecific encounters and usually without advertising song in interspecific encounters. At low general intensities of both drives, a rather pleasant, easily imitated, "pneu" sound is heard. Sometimes in rather high general intensities of both drives a series of faint, high pitched, windy, squealing sounds are uttered which may become more and more rapid, as the attack drive becomes relatively stronger, until they blend insensibly into a faint but perfect rendition of the advertising song.

Bent (1949: 225) describes the advertising song as "a series of four or five downward-inflected phrases with a smooth transition in pitch, the final note prolonged and rolling, and each phrase a little lower than the one before it." The song gives the impression of a descending spiral. During intraspecific encounters (a speaker emitting advertising song) the advertising song seems to be characteristic of relatively high attack motivation. The louder the song from the speaker, the higher the relative escape drive becomes in the bird. By increasing the volume of the speaker while it was being threatened by a territorial male, the bird could be made to flee and, conversely, by turning the volume down, the bird would become emboldened because of its increasing relative attack motivation prompted by the fainter advertising song from the speaker. This was true of all the species (see the May 30 observations given on page 332). By a careful adjustment of the volume while watching the behavior of a bird a point could be reached where the attack and escape drives were judged to be exactly balanced. Under these circumstances the bird would engage in perfunctory preening, bill wiping, "yawning," or some other apparently irrelevant activity. Yawning may be distinguished from Gaping by the context of the act and by the fact that the bill is opened and shut much more quickly in "yawning." Many, if not all, of these are possibly displacement activities, but it is difficult, as I have said, to be sure. What the bird was doing immediately prior to the conflict situation seemed to have something to do with the resulting type of irrelevant activity indulged in. Preening seemed to occur most often in *H. mustelina* as it usually was in some intensity of Spread (very much like the preening postures in many respects) when thrown into a conflict situation between attack and escape. The other species, when in the Horizontal Stretch, would usually bill wipe

or even scratch the head with a foot. I never could induce irrelevant activities while the birds were doing Upwards. Usually the attack and escape drives, even when in balance, were too high for Foot Quivering to occur, so I never observed what a bird might do as a possible displacement at that level of motivations. The following excerpt from my notes is a characteristic observation involving possible displacement activity.

May 28, 1954; Ithaca, N. Y.; 9:15 A.M.; beech-maple woodland near Beebe Lake. Placed a speaker on (*fuscescens*) territory (female building). The speaker was about two meters high in a small maple. I sat on a log about eight meters away. As soon as *fuscescens* advertising song began to play over the speaker, the male (*fuscescens*) flew straight in toward the speaker and behaved in a very agitated manner. He seemed to be looking for an adversary but could not, of course, find one. While he was Wing and Tail Flicking a foot or so from the speaker, I suddenly turned the volume up. He fled instantly. I turned the volume down and he returned. I did this four or five times and then, carefully watching the bird, I turned the volume up slowly until, judging by various flight intention movements, I had the bird "teetering" between attack and escape. At this point he vigorously bill wiped.

The speaker always elicited a quick response when advertising song was played on a bird's territory. A song duel with the speaker typically took place as the bird worked closer to the source of sound. If a model was placed on or very near the speaker the hostile responses were directed at it. If the speaker was used alone the displays were directed at the speaker itself, although not usually as intensely as at a model. A model placed more than two or three meters from the playing speaker generally received little attention. If the speaker was shut off under such circumstances, however, then the model began to receive some hostile attention. This generally did not occur right away, however. Usually a few moments would elapse before the bird "discovered" the model. What probably happens is that the bird takes some time to get rid of its "after discharge" of motivations prompted by the speaker. This period, after intense motivation, may last as long as 15 or 20 minutes, although not nearly as long as this if a model is present to attract attention. Dr. Konrad Lorenz tells me that this is an exceptionally long period for an "after discharge" to last. I am quite sure that the birds were not reacting to the silent speaker as I experimented with each individual but once every few days in order to minimize the effects of any habituation to the experimental procedures, furthermore, the "after discharge" was every bit as long for individuals experimented with the first time.

Hostile vocalizations of the Hermit Thrush (C. guttatus).—The hostile calls of the Hermit Thrush are mainly a rather harsh "chuck"

and a hoarse, canary-like "seeeeeep" with a rising inflection. There is also a thin Cedar Waxwing-like "eeee" (not as mellow or as persistent as a somewhat similar call in *fuscescens*). The "seeeeeep" call seems to be characteristic of low motivation of attack and escape and is followed at higher general motivations, by the "chuck" note and, finally, the "eeeeeeee" calls as attack becomes relatively strong. It is difficult to gain an accurate appraisal of the different calls of these four species as they are not as vocal in their hostile behavior as is the noisy *H. mustelina*.

The advertising song of *guttatus* is a series of fine flute-like phrases similar in some respects to that of *H. mustelina*. Bent (1949: 156) says that the song is "made up of rather long phrases of 5 to 12 notes each, with rather long pauses. All the notes are sweet, clear, and musical, like the tone of a bell, purer than the notes of the wood thrush, but perhaps less rich in quality." It is my definite impression that *guttatus*, except for the advertising song, is the least vocal of these four species.

Hostile vocalizations of the Olive-backed Thrush (C. ustulatus).—The hostile calls of the Olive-backed Thrush are a "peeeep" very similar to the note of the Spring Peeper (*Hyla crucifer*), and which seems most characteristic of relatively and actually low attack motivation, and a rather harsh "chuck-burr" note, strongly reminiscent of a similar note made by the Scarlet Tanager (*Piranga olivacea*), and which seems to be associated with relatively, and/or actually, high attack motivation.

The advertising song of this species is one of the continuous rather than the phrase-type songs. Unlike *fuscescens*, the song seems to spiral upward. Bent (1949: 184) records the song as saying "whip-poor-will-a-will-e-zee-zee, going up high and fine at the close. Sometimes there is an extra a-will."

Hostile vocalizations of the Gray-cheeked Thrush (C. minimus).—The Gray-cheeked Thrush has a harsh "beer" note reminiscent of a similar sound produced by the Nighthawk (*Chordeiles minor*). This note appears to be homologous with the "veer" call of *fuscescens*, a species with which it is rarely sympatric. The "beer" call seems to vary somewhat in pitch and quality depending on the intensity of motivation. There is also a whistled "pneu" note similar to the one given by *fuscescens*, although differing in quality. This sound seems to be associated with low threshold responses.

The advertising song is of the *fuscescens* type. It is of a thinner, windier character than those of the others and does not appear to carry as far. There are two or three introductory notes that cannot

be heard unless the observer is quite near. The remainder of the song follows immediately. Wallace (1939: 309) renders the entire song of Bicknell's Gray-cheeked Thrush as "chook-chook, wee-o, wee-o, whee-o-ti-t-ter-ee." The first two or three notes are slurred downward but in the middle of the song there is a break and the remainder rises in pitch to the end. Unlike the other species, *minimus bicknelli* has a well developed flight song. Wallace (1939: 309) discusses this phenomenon. I have only heard it given during the deep gloom of late evening. This song is essentially like the ordinary song but more rapid. On the few occasions when this song was given while it was yet light enough to see, the bird rose on rapidly beating wings from the stunted balsams and swiftly circled around over the tree tops giving its flight song the entire time. When finished, the birds drop abruptly back into the trees, often only to take to the air again immediately and repeat the entire performance. Several birds may be in the air at once and little regard for territorial boundaries is observable. Birds down in the thick spruce and balsam cover constantly utter high intensity "beer" calls and ordinary advertising song. Much more study is necessary before the exact nature of these occurrences will be understood. The following extract from my notes provides a typical observation on flight song.

June 12, 1953; Whiteface Mt., Essex Co., N. Y.; 8:45 P.M., cool, breezy and overcast. Wisps of mist blowing up from below through the stunted balsams and spruces. Nearly dark. Many (*minimus*) singing all around. One individual could be dimly seen as it rose straight up from the concealing vegetation on rapidly beating wings, it then straightened out and swiftly flew around over a considerable area (about 30 meters in diameter) uttering a continuous variation of the advertising song. In about 10 seconds it dropped abruptly into the thickets. Others could be heard engaging in this flight song but were only dimly seen twice. The thickets concealed what sounded like dozens of individuals giving ordinary advertising songs and uttering loud "beer" calls.

Like many species, those of *Catharus* and *Hylocichla* have two main song periods during the day; one in the evening and the other in the early morning. Unlike many species, however, the more active period is in the evening. This is most noticeable in *minimus*. Its periods of most intense activity are short in duration but very intense and occur chiefly just after sunset and just before sunrise. These periods of intense activity are only about 20 minutes to a half hour in duration but may be a little longer on cloudy days. All of these species may be heard to utter advertising song and other vocalizations at night, but *minimus* appears to do this most frequently and, as a matter of fact, seems more vocal during the night than during the middle of the day.

Explanation of hostile behavior diagrams (Figures 6 and 7).—The hostile behavior of *H. mustelina* is diagrammed in Figure 6 and that of the four species of *Catharus* in Figure 7. Increasing general intensities of attack and escape motivations (actual strength) are plotted from the bottom of the page to the top. Displays most closely associated with varying degrees of attack motivation are plotted to the left of the line indicating increasing general intensities of attack and escape drives, and displays most closely associated with increasing relative strength of escape motivation are plotted to the right of this line. By studying these diagrams it may be seen that the relative strength of one drive may be quite low even though the actual strength of both drives may be very high and also it may be noticed that the actual strength of one drive may be quite high although the relative strength is low. Two ideas must be kept in mind if a full understanding of the diagrams is to be attained. One is that the postures listed along the line of general intensity of both drives might best be imagined as being slightly skewed toward the attack side; more so as the motivations rise. The other is that the various behavioral patterns are not as canalized as the diagrams may appear to make them. The arrows merely indicate the directions of increasing intensities of the actual and relative strengths of the drives. The various strengths, actual and relative, can fluctuate back and forth in an infinite variety of combinations and expressions within the framework diagrammed.

Wing and Tail Flicking, without the Spread posture, in *mustelina* is indicative of rather low intensity of both attack and escape drives (see field notes on pages 327 and 328). My captive birds commonly performed Wing and Tail Flicking and only rarely adopted the Spread which was generally in response to a passing dog or other animal. If the escape drive becomes much stronger than the attack drive, simple fleeing takes place, as it apparently does from any hostile motivational level in this species. If the attack drive is stronger than the escape drive, the bird may perform any of the displays associated with a relatively high attack motivation, depending on the relative amount of this motivation. If the attack drive is relatively low, simple Supplanting is most likely to result. If the attack drive is relatively higher, Bill Snapping, Winnowing, and vocalizations may result, as well as Supplanting. The hostile motivational level may rise to the levels typified by the various degrees of Spread. Here, the same thing occurs depending upon which, if either, of the drives becomes relatively stronger. It is possible, in all of the species, for the hostile motivation to rise with both drives in

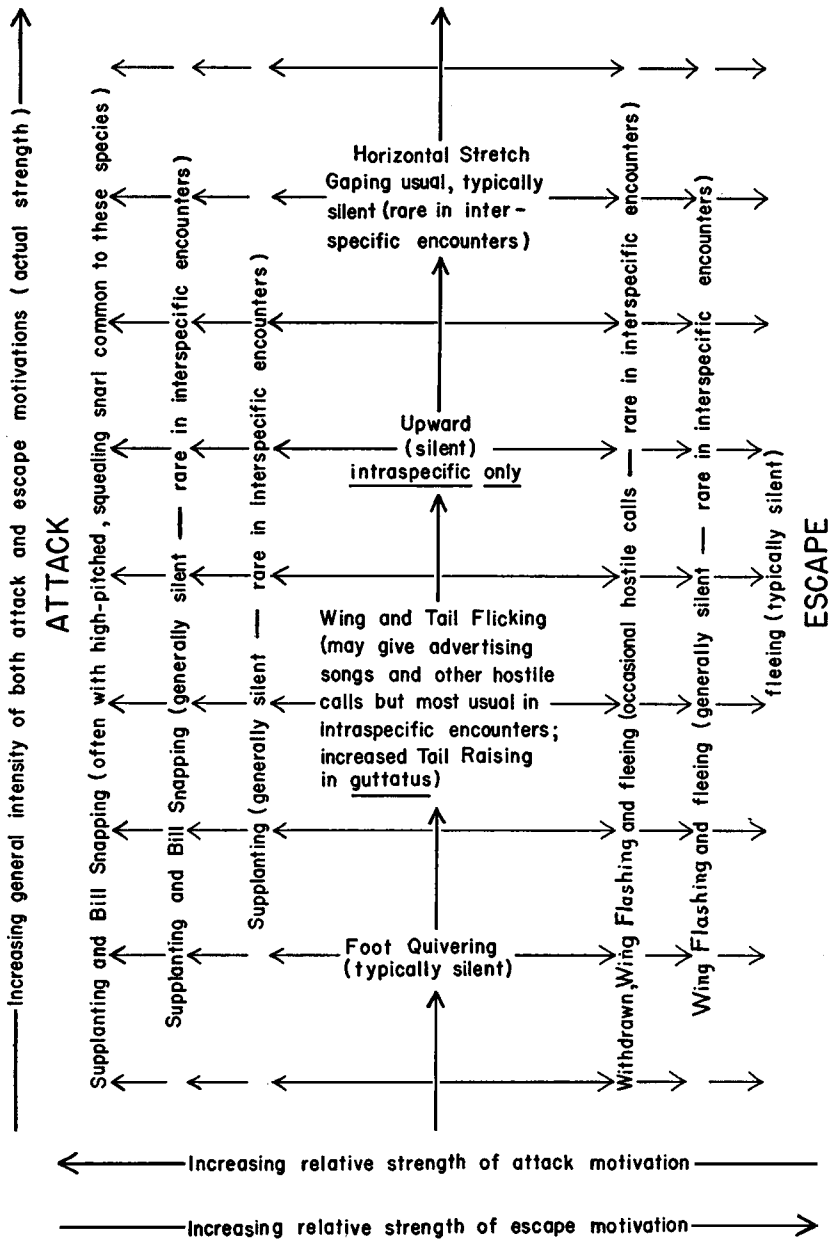


FIGURE 7. Diagram of the hostile display patterns of *Catharus fuscescens*, *C. guttatus*, *C. ustulatus*, and *C. minimus*. See text for explanation.

virtual balance and then diminish without any overt display clearly associated with either attack or escape. This would most likely occur in intraspecific situations rather than interspecific situations (see below).

The same interplay of relative and actual levels of motivation is true also for the other four species (Figure 7). During interspecific encounters, however, the Upward is omitted. It is interesting to note that these species have more postures associated with relatively higher escape motivation than does *H. mustelina*. The behavior in general appears to be more complicated and this may indicate that, as far as hostile behavior is concerned, they are more primitive. This type of hostile behavior is much more like that found in non-passerine birds such as the ducks (Lorenz, 1951) and the gulls (Moynihan, 1955a; Tinbergen, 1953). In regard to hostile behavior, these four species resemble a fish, the Three-spined Stickleback (Tinbergen, 1948), more closely than they do birds such as the Estrildine ploceids, for example, Black-headed Nuns, *Lonchura punctulata* (Moynihan and Hall, 1954); Spice Finches, *L. ferruginosa* (Moynihan, pers. comm.); and Zebra Finches, *Poephila guttata* (Morris, 1954). It seems possible that the simpler hostile behavioral patterns are more specialized than are the more complex ones such as demonstrated by the four *Catharus* species.

Comparison between intraspecific and interspecific patterns.—There is a tendency toward fewer displays associated with interspecific encounters than are typically associated with intraspecific encounters. Many of the displays associated with interspecific encounters also tend to be of shorter duration. This may be due to the fact that the drives are less often in approximate balance during interspecific encounters, or it is possible that the releasing thresholds of the hostile displays have been shifted. The Upward is omitted in interspecific encounters by the four *Catharus* species and the Horizontal Stretch, Withdrawn, and Wing Flashing are rare. Silent Supplanting is rare in *mustelina* during interspecific encounters. Spreads are typical in interspecific encounters but are usually shorter in duration than they are in intraspecific encounters.

It is probably biologically advantageous to have a reduction in the displays associated with interspecific encounters in case the opponent releasing hostile behavior is physically dangerous. In addition, most of the displays are probably not mutually "understood" interspecifically and therefore their employment is probably selected against unless there are definite selective pressures for their use derived from competition. The interspecific hostile displays which

occur among the species of thrushes studied seem mainly those they possess in common. The hostile displays seen in various combinations of species including *Turdus migratorius*, *Sialia sialis*, *H. mustelina*, and these four *Catharus* species are Gaping (all of these have bright yellow mouth linings), Wing and Tail Flicking, Supplanting, and simple fleeing. More interspecific displays are seen in captive birds than are typical of wild situations, but in captivity the birds are unable to flee far and are forced into an unnaturally great amount of competition over food, water, and space. This may result in a greater amount of conflict between the attack and escape drives. Even under these conditions, however, the Upward is not seen in interspecific encounters.

SEXUAL RECOGNITION AND PAIR FORMATION

Since the sexes in *Hylocichla* and *Catharus* cannot be distinguished by their external appearance, behavioral clues were assumed to be utilized by the birds to facilitate their sexual recognition. Allen (1934), working with the Ruffed Grouse (*Bonasa umbellus*) and Nice (1943), working with the Song Sparrow (*Melospiza melodia*) have shown that behavioral patterns are responsible for sexual recognition in these species.

Males of all of the species of *Catharus* and *Hylocichla* arrive on the breeding grounds ahead of the females and set up and defend territories against birds of their own species. The females, after arrival, attempt to invade the territories belonging to males of their own species. This invasion elicits hostile behavior on the part of both the resident male and the intruding female. The principal differences between the behavior of a trespassing male and the newly arrived female is that the former almost always flees from the attacks of the resident male and an intruding female tends to flee but persists in remaining within the resident male's territory. This leads to a situation where much mutual hostile displaying occurs, since the drives of both birds are strong and typically in fairly close balance. In addition, the male's hostile behavior is augmented by a noticeable increase in advertising song. This is a territorial defense reaction to the intrusion by the trespassing female, but at the same time it probably raises the level of her motivation to remain. Her sex drive may be an important stimulus here.

Since it is usually impossible to distinguish the sexes in the field unless a bird utters advertising song, it was difficult to understand much of the behavior seen. Consequently, an effort was made to collect as many as possible of the fleeing birds engaged in intraspecific encounters.

Seventeen such fleeing birds were collected; *Catharus minimus*, 1; *C. ustulatus*, 5; *C. guttatus*, 4; *C. fuscescens*, 5; and *H. mustelina*, 2. Ten of these specimens had fled from the resident male's territory and proved, upon dissection, to be adult males themselves. Five of these specimens did not flee from the territory of the resident male but, instead, persisted in remaining within its boundaries; all of these proved, upon dissection, to be females. The remaining two specimens require comment. One, a female *mustelina*, had fled straight away from the resident male's territory and showed no indication of being motivated to return. In this case the bird may have already been mated and was really trespassing, or the male may have had a mate. The other case was a female *guttatus* that fled straight away upon receiving an Upward and Horizontal Stretch (in that order) from the resident male, but this bird could not be collected at that time and before I could get a clear shot she had returned and was being chased around and about his territory.

Since the female, when being chased by the male, tends to remain within his territory, more or less circular flights result. These have been termed "courtship" in various places in the literature, e.g., Bent (1949: 104). Early in the pair-formation period these flights tend to be "wild" and clearly associated with attack and escape motivations, but in a day or two they become progressively more leisurely and even approach a condition that might be described as sedate. Here the birds fly rather slowly and deliberately. In the four authenticated cases (the pursuer or both birds being collected) the pursuer was always the male. Frequent pauses are made during which the birds perch about the same distance apart as they were when flying. They remain motionless for a few seconds until the leisurely pursuit is resumed. I have watched a pair of *mustelina* engaged in this behavior at a time when the female had a completed clutch of eggs. The pair bond seems to be formed when the progressive lessening of mutual hostility reaches a point where the male more or less accepts the female on his territory. This period seems to take three or four days in all of these species. The following, taken from my notes, will illustrate typical observations on the pair formation period.

May 15, 1953; Ithaca, N. Y.; 2:30 P.M. in beech-maple woodland. . . . female(?) (*mustelina*) being chased all around about through territory by male. Chase very swift and erratic. No vocalizations heard.

May 18, 1953; (same locality as above) . . . female (same one seen on 15th?) carrying nesting material to crotch in small maple sapling. Nest looks as though it was just begun. No mud as yet.

June 16, 1954; Whiteface Mt., Essex Co., N. Y.; 7:00 A.M. in dense balsam thicket. Two (*minimus*) engaged in wild circuitous flight around bases of balsam trunks,

very close to ground. The pursued bird seems to be motivated to persist in remaining in vicinity which may be male's territory.

June 19, 1954; (same locality as above, 6:30 A.M.). Two individuals (*minimus*) seen foraging together in same area. I was unable to collect either bird but they seemed to be a mated pair.

This type of pair-bond formation is quite similar to that of the Willow Warbler, *Phylloscopus trochilus* (May, 1949). Hostile behavior may be observed between a mated pair throughout their time of association. Individual distance apparently is overcome completely only during copulation and then only because the attack and escape drives of both birds are temporarily suppressed by the sex drive. Conder (1949) discusses the phenomenon of individual distance and visualizes it as a sort of mobile territory each individual bird carries about with it. This seems to consist of the area the bird can reach all about itself and within which does not willingly allow other birds to trespass. This behavior pattern is responsible, for example, for the regular spacings of birds in flocks. A few forms seem secondarily to have lost this pattern and will allow close bodily contact with one another, for example, some swifts and colies. Hinde (1955) is convinced that in the Chaffinch (*Fringilla coelebs*) and the Greenfinch (*Chloris chloris*) the escape and sex drives are in conflict in mated pairs. In the case of these thrushes it does not seem to be as clear that escape is the element in principal conflict with the sex drive. Escape and attack seem to be about equally in conflict with the sex drive.

There seems to be little doubt that individuals of a pair come to recognize one another. Males do not threaten their mates when they appear after an absence, although strange birds of their species receive prompt attack. Birds of a pair sometimes threaten one another when individual distance is being violated "deliberately" (as in unsolicited copulation attempts) or "inadvertently" (as in coming to the nest with food at the same time). The following notes will typify these responses.

May 27, 1954; Ithaca, N. Y.; Territory No. 13 in edge of beech-maple-hemlock woodland along Cascadilla Creek, 9:30 A.M. . . . male (*mustelina*) singing in top of small beech tree near nest. Female not in sight. In a few minutes the female flies to sapling near nest, male sees her but did not even Crest Raise. He continues to sing, female settles on eggs.

June 19, 1954; Ithaca, N. Y.; Territory No. 6 in second growth edge surrounding small beaver pond. 7:00 A.M. I examined (*guttatus*) nest on ground under fern clump. Female flew off and disappeared. I retire and wait. Male singing nearby and gradually he comes into view. After a few minutes elapse he flies to edge of nest and appears to be regarding the eggs. The female suddenly flies down to

ground near nest and Tail Raises, the male simply flies upward to nearby hemlock and commences to sing.

June 12, 1954; Ithaca, N. Y.; Territory No. 3 in wet bottomland woodlot . . . (*fuscescens*) foraging on forest floor and in low bushes. It hops to top of rotten, moss-covered, fallen log and begins to preen. Another individual suddenly appears on log and hops toward first bird. The second bird attempts to mount the first bird which receives these attentions with Horizontal Stretch and Gaping.

May 30, 1953; Ithaca, N. Y.; Territory No. 1 in second growth beech-maple forest on shore of Beebe Lake. . . . young (*mustelina*) have hatched and being fed by parents. One adult flies to nest with beak full of what appears to be geometrid larvae but before feeding takes place, the other bird flies in with beak full of same food. The first bird threatens the newcomer by Gaping, the food then drops to ground and the bird flies down to recover it and in the meanwhile the threatened bird, which did not flee when threatened, feeds young and flies away. In a moment the bird that had dropped its food returned to nest with what looked like most of it and fed young.

SPECIES RECOGNITION

The various species of *Catharus* and *Hylocichla mustelina* are all readily identifiable by a human observer, but the difference in size, color, and pattern are not great. It is not clear that differences of size and plumage serve as specific recognition features in these forms, although some observations in the wild and with captive birds indicate that the reddish tail of *guttatus* and the reddish crest of *mustelina*, if accompanied by their characteristic displaying movements (see above), serve as species-specific recognition features (see the May 30 observation on page 335, for instance). The only thing really different among these forms is their vocalizations. These were assumed to serve as the chief specific recognition signals, and a series of experiments was conducted to determine the validity of this assumption.

The first experiments consisted of placing blank models on the territories of each of the species. The following numbers of territorial males were tested and all were either in the pair-formation period or shortly thereafter: 10 *mustelina*, 6 *fuscescens*, 4 *guttatus*, 5 *ustulatus*, and 2 *minimus*. All of these males either did not appear to "notice" the models at all or merely accorded them the same reactions that any strange object typically receives (some slight tendency to "investigate" and perhaps very low intensity Crest Raising or Foot Quivering). The blank models used were simply unpainted examples of the models ordinarily used in these behavioral experiments. The color was a uniform off-white or ivory and with black eyes.

The next experiments consisted in introducing naturally colored models of each of the five species on the territories of each of the species. In this series of experiments 10 *mustelina*, 8 *fuscescens*, 8 *guttatus*, 7 *ustulatus*, and 5 *minimus* territories were utilized in this manner.

All of these males were either in the pair-formation period or shortly thereafter. Care was taken to present the bird's own species model to him last in the series so that any possible "after discharge" of activity in response to his own species would not effect subsequent presentations. This was probably unnecessary in this case as all of the models, without exception, were attacked more or less vigorously. Sometimes a male would attempt coition with a model that had been placed in a position too nearly horizontal (simulated submission posture) but the reactions were clearly attack associated with a relatively high attack motivation. No greater attack seemed to be elicited by conspecific combinations although this would be difficult to be sure of without quantitative data and these hostile behavior patterns, for the most part, would be difficult to quantify (see Figure 8).

The final experiments consisted of placing models associated with advertising songs and other hostile vocalizations in every combination on territories of all five species. The results are summarized in Figure 8. The territories of 20 *mustelina*, 11 *fuscescens*, 12 *guttatus*, 15 *ustulatus*, and 10 *minimus* were all treated to at least one such series of experiments. This was a time-consuming operation as usually only one combination of vocalization and/or model was presented to any one territory on any given day in order to minimize the dangers of habituation to the experimental procedure. Consequently, these territories were being worked with in every state of development from the pair-formation period to the time when the young were nearly fledged. It may be seen by an examination of Figure 8 that the models, when associated with vocalizations, were no longer attacked indiscriminately but only attacked when associated with vocalizations of the species being experimented with. For instance, no model associated with vocalizations was attacked by a male *ustulatus* unless associated with *ustulatus* vocalizations.

Slight attack (Wing and Tail Flicking, Crest Raising, and generally behavior typified by increased "agitation") was elicited occasionally when the "veer" calls of *fuscescens* was played to *minimus* and when the "beer" calls of *minimus* were played to *fuscescens*. These two calls are apparently similar enough to act as releasing stimuli for the (innate) releasing mechanisms of the other species. These two species rarely occur sympatrically so that few mistakes as to species identity, however slight, are likely to take place. At any rate, pairing has taken place in *fuscescens* before *minimus* migrates through the areas occupied by the former species. This would be the only time these two species usually occur together, and it is conceivable that an occasional unpaired *fuscescens* might respond to the vocalizations

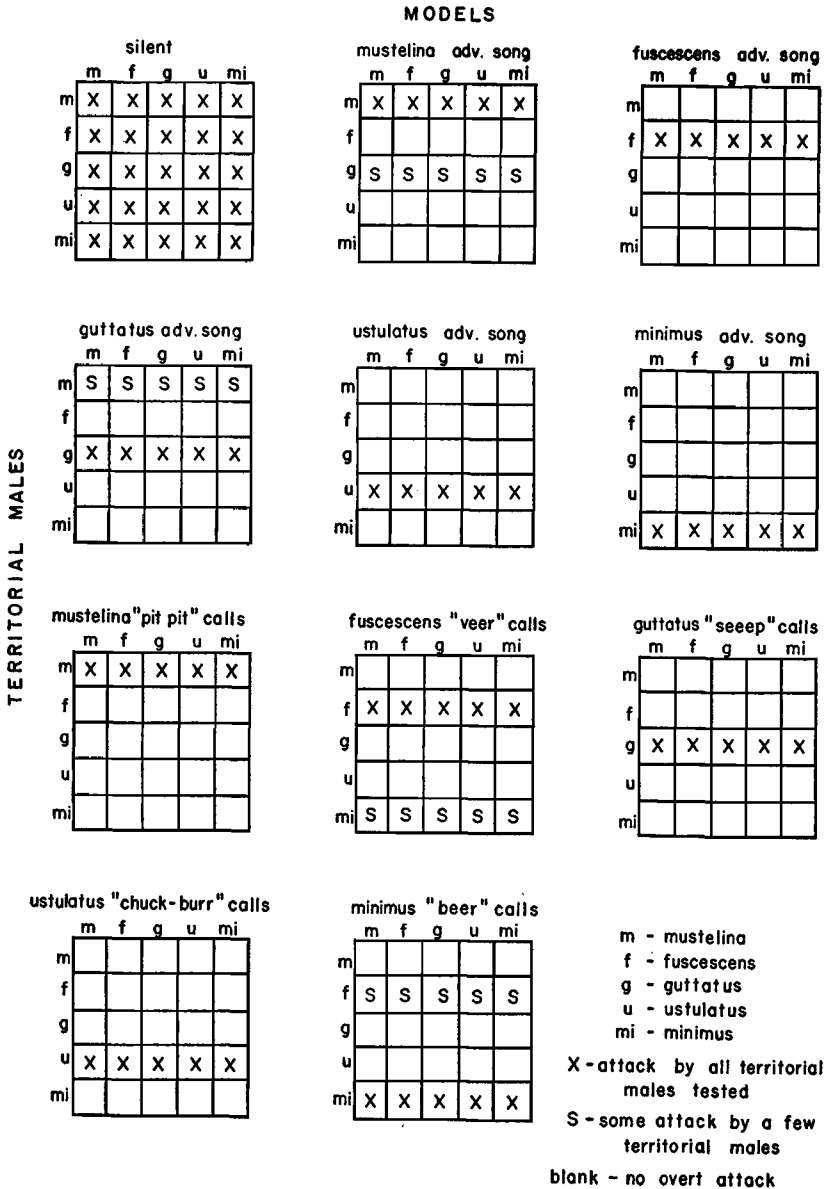


FIGURE 8. Diagram of results of experiments with models and/or hostile vocalizations on territorial males of *Hylocichla mustelina*, *Catharus fuscescens*, *C. guttatus*, *C. ustulatus*, and *C. minimus*. See text for explanation.

of *minimus*. The converse is also possible. The chances of mixed pairs being formed must be almost nil as all of the other secondary species specific signal characters would be lacking and also the physical environment and physiological states would not be compatible. Since these two species rarely occur sympatrically there seldom has been any selective pressures on either to make for greater divergence in this particular call, and the fleeting contact they do have may even supply enough selective pressure to maintain this similarity through slight ecological competition.

The somewhat similar advertising songs of *guttatus* and *mustelina* sometimes released a response in the other species. Here again, the mixed reactions involved only a few individuals and the hostile behavior seemed to be of low intensity. The chances of mixed pairs being formed in this situation is made slightly more likely since these two species are more often sympatric. However, as in *fuscescens-minimus*, the secondary species-specific signal characters would be different; vastly different in this case, as much of the hostile behavior of *mustelina* is entirely different from that of *guttatus* and the rest of the group. The greater size of *mustelina* coupled with differences in color, pattern, and habitat should further reduce the chances of long-term mistakes.

Advertising song and other hostile vocalizations were presented in every possible combination to territorial males without the use of models (see May 28 observation on page 338). Here the hostile reactions were the same as when models were used in conjunction with vocalizations but were not quite as intense, although very much more intense than when silent models were presented. It seems quite clear that vocalizations are much more effective as species specific signal characters than are the differences in physical appearance.

The various species of *Catharus* and *Hylocichla mustelina* have "solved" their problems of species recognition in sympatric situations in much the same manner as *Anas*, except that the species-specific signal characters are largely vocal rather than mostly visual. The reason for this difference in the kind of signals employed may be that the selective pressure by visual predators is great enough to cause both sexes to become cryptically colored so that non-visual signals have been evolved. I think it more likely, however, that it is mostly a matter of efficiency in regard to ready recognition. Visibility is limited in the habitats utilized by *Catharus*, and auditory signals would be evolved because of their greater effectiveness in situations characterized by low visibility. The minor differences in plumage and the small differences in thresholds of the various displays, prob-

ably act as fortifying features to the species-specific auditory signals. The dabbling ducks, on the other hand, form pairs in areas where the visibility is relatively great and visual signals can operate to full advantage. It is not that auditory signals are completely ineffective in open areas or that visual ones are useless in areas of limited visibility, but it is a matter of relative values. The genera *Anas* and *Catharus* both utilize auditory and visual species-specific signal characters but the most effective ones in each case have become predominant.

The experimental evidence indicates the manner in which *Catharus* and *Hylocichla* males recognize their own species; but does not prove that the females react in the same way. The evidence here, supported by what we know of the reactions of males, is that females do not distinguish between models of various *Catharus* species and that the various vocalizations are the only striking differences to be noted among these forms that could serve as species-specific signal characters. The hostile displays, with the exception of the well developed advertising songs in males, are the same for both sexes of a given species—there are no known well-marked visual species-specific signal characters in *Catharus* and *Hylocichla* except for the reddish tail and its movement in *guttatus*, the brilliant yellow base of the mandible in *minimus*, and the reddish crest and its movement in *H. mustelina*. These visual characters are probably valuable at close range but of little use in the initial drawing together of pairs. Many birds have been observed at the initial stages of pair formation and no mixed pairs have ever been seen.

What apparently happens in *Catharus* and *Hylocichla* is that females “home in” on advertising songs of males of their own species. These advertising songs have evolved as species-specific signal characters to which the females have evolved specific releasing mechanisms. When the female is in visual contact with her prospective mate other species-specific characters fortify the initial choice. The proper habitat probably also is an important factor in minimizing the possibility of mixed pairs being formed as is the differential in breeding times demonstrated by some of the species.

SUMMARY

A comparative study was conducted on the hostile behavior of the four North American species of *Catharus* and on *Hylocichla mustelina*. These behavior patterns are described and evaluated. The hostile behavior patterns of *H. mustelina* are quite different from those of the four species of *Catharus*. These latter hostile behavior patterns, excepting vocalizations, are similar to one another.

Experiments conducted with tape recordings of the hostile vocalizations and models of the various species provided most of the data utilized.

It is suggested that the principal reproductive isolating mechanisms, preventing mixed pairing among these species, are the species specific vocalizations of the males (advertising song) acting as sign stimuli to the corresponding specific releasing mechanisms of the females. Minor differences of plumage pattern, color, and movement probably play roles fortifying the initial choice.

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