AN AGGRESSIVE DISPLAY AND RELATED BEHAVIOR IN THE LOGGERHEAD SHRIKE

Susan M. Smith

THE Loggerhead Shrike (*Lanius ludovicianus*) is territorial virtually year-round. During the nonbreeding season each individual defends its own hunting territory; after pair formation each member shares in the defense of the nesting territory (Miller, 1931; Bent, 1950).

Territorial spacing may be achieved in two ways: either by fighting or by some sort of aggressive display. As fighting may result in injury even to the winner, any form of behavior that allows dominance to be established without physical combat may be expected to have some selective advantage. The ritualized displays most bird species use in territorial encounters are generally thought to have evolved as a result of this type of selection (see, for example, Marler and Hamilton, 1966: 178). The strength of this selective force will vary with the species; Lorenz (1952, 1966) points out that such selection will be strongest in highly gregarious species, and in those most capable of inflicting injury to each other in physical combat.

Loggerhead Shrikes regularly kill birds as prey. Probably most of these are the size of a sparrow or smaller, yet shrikes of this genus occasionally attack birds their own size or even larger. Bent (1950) reported a Loggerhead Shrike killing and eating an adult Mockingbird (Mimus polyglottos), and Ellison (1971) wrote of a Northern Shrike (Lanius excubitor) attacking (unsuccessfully) an adult female Spruce Grouse (Canachites canadensis). The attack on the Mockingbird is particularly significant in light of the similarity in size and color pattern between predator and prey. Furthermore Loggerhead Shrikes direct their attack precisely to the back of the neck (Miller, 1931; Smith, 1973); shrikes can kill a full-grown house mouse with a single peck. This pattern of attack is also used for bird prey; presumably one shrike could seriously injure or even kill another with a single peck in the same manner. This ability could provide very strong selection for displays that minimize contact in aggressive situations, even in this nongregarious species. The present report indicates that the wing-fluttering display, described below, serves exactly this function.

METHODS

Five broods of Loggerhead Shrikes totalling 30 birds were hand-reared in the spring of 1967. These were kept in cages made of ½-inch hardware cloth attached to wooden frames approximately 30 inches long and 20 inches in height and breadth. Most cages contained either 4 or 5 birds; one had only 2 birds. Later



Figure 1. The flutter display. The angle formed by the birds is approximately 130 degrees.

the shrikes were transferred to outdoor aviaries on the University of Washington campus in Seattle. These were all 12 feet long, 9 feet high, and 6.5 to 8.5 feet wide. No more than four birds were placed in any aviary. The shrikes were kept in the aviaries all winter and released in March 1968. The captive shrikes' displays were recorded on 16 mm black-and-white moving picture film.

In addition I made field observations on a wild population of shrikes in central Washington from mid-March to mid-June 1968. This period covered the complete nesting cycle from nest building through the breakup of the first-brood family flocks.

RESULTS

DESCRIPTION OF THE FLUTTER DISPLAY

A shrike gives the display only when another shrike is present, usually within a few feet of the displaying bird. Although sometimes only one bird gives the display, usually both birds perform simultaneously. Displaying birds typically face away from each other, except when the birds whirl to face each other before a chase or fight. The angle formed by the birds is usually between 60 and 120 degrees (Figure 1).

The displaying bird holds its body in a horizontal position, sometimes flexing its legs so extensively that the entire tarsi are flat on the ground. The wings are drooped slightly away from the body, and fluttered rapidly. The back feathers are raised, and the head is lowered; frequently the bird pecks the ground or perch forcefully and repeatedly. The tail is always spread, the extent varying with the intensity of the display. The crown feathers are usually depressed. The displaying bird may be silent, or may give a rising note similar to that made by a juvenile shrike begging for food, but recognizably harsher in quality. Within the limitations of the perches, one or both birds may perform much maneuvering of position; this may be accompanied by loud stamping, especially on flat surfaces. For simplicity, I refer to this behavior as the "flutter display."

OBSERVATIONS ON CAPTIVE BIRDS

I saw captive juvenile shrikes performing the flutter display first when they were 33 days old. By the time they were 50 days old, all of the young shrikes regularly gave this display in competitive situations for access to a resource such as a perch, bath, or food. Even at this early age, the shrikes always followed their flutter displays either by some overt aggressive act such as allopreening, pecking, or chasing, or by the retreat of one of the birds.

On 12 September 1967 I transferred the shrikes from their cages to the outdoor aviaries. Within a few days the birds established individually defended areas within the aviaries. In such small enclosures, invasions were frequent, and the most commonly seen display in these disputes was the flutter display. I saw these daily throughout September and October, and sporadically through mid-December; after the beginning of January the social relations of the birds were firmly established and they rarely used the display. In every aviary containing four birds, I saw each bird perform the flutter display at least once with every other bird.

During this time I watched over 60 such displays, many from very short distances. Each aviary connected to a small building with a window of one-way glass. Occasionally shrikes performed flutter displays close to these windows; Figure 1 was drawn from films taken through them.

The displays mentioned above were all between members of the same brood that had always been together. In January 1968 an encounter was staged between two birds from different broods in one of the smaller aviaries that was strange to each of them. Both had been injured the previous month and had been removed from their former aviaries and kept in separate small cages until they had fully recovered. As soon as the second bird was placed into the aviary, both birds began the flutter display, calling loudly and pecking hard at their perches. Often the displaying birds were several feet apart and at different heights; yet even when separated they never faced each other while displaying. The encounter lasted for 3 hours. Within the first hour two fights (i.e. encounters involving physical contact) occurred; in the second of these the attacker was calling loudly just before the fight, while the other bird was displaying silently. After the first 90 minutes only the bird that had initiated the attack in both fights still gave the flutter displays. The other bird, with increasing frequency, adopted a long, thin, upright posture, with all its feathers pulled in, head up, and facing its opponent (Figure 2). This second posture was entirely distinct from the flutter display; I have never seen a shrike in a position that I could interpret as being intermediate between the two. Periodically the apparently dominant bird broke off its flutter display and chased the other bird around

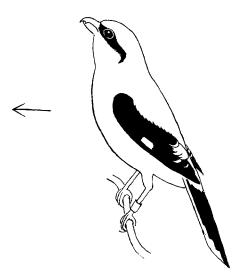


Figure 2. Posture assumed by subordinate shrike near the end of the staged encounter. The arrow indicates the location of the dominant bird.

the aviary. These chases occurred with increasing frequency until I removed the subordinate bird.

OBSERVATIONS ON BIRDS IN THE FIELD

When field work began in mid-March of 1968, the shrikes were already paired and on territories, but nest building had not yet begun. Nine territories were mapped. The bluish males were readily distinguishable from the relatively brown females. Variations in plumage such as amount of white in the wings and tail and lost feathers permitted individual recognition of all 18 resident shrikes.

Much of the territorial behavior seen even in March consisted simply of loud songs and "bzeek" notes (Miller, 1931) when an invading shrike appeared. If the invader remained, the resident then chased it briefly. This was the usual pattern between members of neighboring pairs.

I saw wild adults perform the flutter display on four different occasions. These were all relatively early in the season: once on 29 March, twice on 30 March, and once on 2 April. Each instance involved a different resident pair; none of the invaders was from the eight surrounding territories, and they may have been migrants. Three of the four encounters involved only males; in the fourth the resident female gave a flutter display to an invading male, then both resident birds chased the invader from their territory. The encounter of 29 March serves as a sample case:

08:23: a pair of shrikes from outside the study area invade the territory of an established pair. 08:25: the resident male sings loudly, then chases the invaders behind a cliff. 08:45: the invaders return, and are chased by the resident male who gives "bzeek" calls during the chase. 09:05: the invaders reappear; the male lands on the edge of a cliff within a few feet of the resident male. Both immediately give full flutter displays, each calling loudly and pulling repeatedly at grass growing at the edge of the cliff. The two birds form an angle of approximately 60 degrees. The display lasts almost 30 seconds, and ends when the two whirl, dash together, lock feet, and fall together to the base of the cliff. The fall separates them and the resident chases the invader out of sight. 09:33: the invader sings from a distant cliff; the resident flies to the site of the previous fight and gives several "bzeek" calls. The invader immediately approaches and both birds give flutter displays, lasting approximately 15 seconds. The invader breaks off and flies up to an unusually high elevation; the invading female joins him, and both fly northward out of sight, maintaining their high elevation. The resident male sings briefly from the cliff, then joins his mate near their nest.

This contact fight was the only one I saw in approximately 16 weeks' field work over a 3-year period. All other territorial encounters seen during this study were boundary disputes between neighboring pairs. No flutter displays were seen between two known birds, although these probably occurred in early March when the breeding territories were originally established.

I also saw wild juvenile shrikes performing the flutter display in the spring of 1968. The horizontal posture and bowed head, along with the strident quality of the call, made the display easily distinguishable from begging for food. The youngest bird I saw perform this display was 32 days old, only 1 day younger than the age at which captive shrikes were first seen giving the display. I followed two broods closely until the family flocks dispersed; this occurred in both broods by their 41st day. During this period I made 11 more records of flutter displays between young shrikes; the last 5 ended in chases.

COURTSHIP FEEDING

Of 42 records of courtship feeding from 9 pairs between 22 March and 16 May, the first 31 (all before 19 April) involved neither wing-fluttering nor calls of any kind by either bird. Begging notes occurred on only 7 occasions: 5 by the female and 2 by the male before feeding. In each of these instances, the young had hatched before begging and fluttering were used in courtship feeding. Furthermore territorial boundaries had been established for several weeks. The last recorded territorial flutter display occurred 17 days before the first fluttering during courtship feeding.

Even when fluttering and begging notes did appear in courtship feeding, the performance differed from the flutter display because the birds faced each other, the female's head pointed up, and the call was more similar to that of a hungry fledgling than that of a territorial adult.

DISCUSSION

Interpretation of the Flutter Display

Captive birds.—In both the small cages and the larger aviaries, the flutter display was definitely correlated with aggressive situations. It was the only display associated with the establishment of the defended areas within the aviaries; the display became less frequent after these territories were firmly fixed.

The data from the staged encounter between two strange birds contained several points of interest. First, even though in the other aviaries the flutter display was rare in January, it was immediately given by two strangers when they met in unknown territory. Secondly, just before the second fight the attacker was calling loudly while the other bird was silent; hence the calls appeared to be aggressive rather than submissive in nature. Thirdly, the posture the subordinate bird assumed toward the end of the encounter was particularly interesting. Virtually every aspect of this position was the direct opposite of the flutter display (Figures 1 and 2). Also, the bird was silent when in this position. This may be another instance of Darwin's principle of antithesis, such as Marler (1956) has shown for Chaffinches (*Fringilla coelebs*): in such cases a posture that is most directly opposite to the threat posture is most likely to inhibit attack.

Finally it might at first glance seem strange that the two birds did not merely set up exclusive territories within the aviary, especially as four birds were living relatively peacefully in another aviary of the same size. It is uncertain whether this was due to the fact that the birds were strangers, or to the fact that each had been kept in isolation for several weeks prior to the encounter. A normal individual winter hunting territory is far larger than the size of an aviary; probably it is more surprising that groups of four shrikes were successfully maintained all winter in aviaries of this size.

Wild birds.—In the present study, wild adults were seen giving the flutter display only early in the breeding season, and only when their territory was invaded by apparently unknown shrikes (as opposed to known neighboring birds). The flutter display preceded the only fight seen in the study; in all other cases it resulted in a chase. Although each sex can perform the display, it was most often performed during the breeding season by two male birds. Hence it seems apparent that this behavior is an aggressive display ordinarily involved in territorial

defense. Further, its use may be restricted to only the most highly aggressive situation, i.e. close approach of an unknown shrike.

Miller (1931: 151) published an account of behavior by Loggerhead Shrikes that bears striking resemblance to the flutter display, although he interpreted it very differently. He wrote: "On the morning of November 30 a shrike noted in this territory and watched for a short time was soon seen to be violently chased high in the air by the apparent owner of the area. The chase was accompanied by the sharp note, bzeek, several times repeated, indicative of excitement and usually associated with combat. The intruder was followed to the edge of the territory whereupon the defender [italics mine] stopped and engaged in a sex display commonly seen during the breeding season. This consisted of fluttering the wings and of begging notes similar to the actions of females during the laying and incubating periods." Miller shot the bird that had been driven away; it was a male. He assumed the territory owner was a female, which may well have been true, and remarked that "such mating activities" occurring before the winter solstice were unusual. Indeed this is so. However if the above account is interpreted as being a flutter display, then it appears to be simply an example of ordinary territorial defense. Elsewhere in the same paper Miller showed that single shrikes defend individual territories during the winter.

Hence the evidence suggests that the flutter display is involved with the defense of both breeding territories and individual winter territories.

RELATION TO COURTSHIP FEEDING

Many aspects of the flutter display resemble typical passerine court-ship feeding. In many species during courtship feeding, the female quivers her wings and gives begging notes before being fed by the male. Miller (1931) stated that this is also true for Loggerhead Shrikes. Especially during late nest building and egg-laying, he wrote, the female follows the male, "rapidly fluttering her wings, posturing, and uttering begging notes" (p. 167). He further wrote that as the season progresses, the female's begging becomes less pronounced: "Her begging notes are less intense and, although the wings are fluttered, the tail is not spread and there is no squatting or posturing" (pp. 174–175). This is exactly the reverse of what occurred in the study population in central Washington in 1968. Of 42 records of courtship feeding, the first 31 involved neither wing-fluttering nor vocalizations of any kind. Only after incubation was over and the young had hatched were fluttering and occasional begging notes seen associated with courtship feeding.

Possibly the difference in behavior between Miller's population and that of the present study is due to difference in latitude. Miller's popu-

lation in California was towards the southern extreme of the range; the birds there were resident, and in the winter migrants added to the population. The population in Washington is very close to the northern extreme for this subspecies (Miller, 1931) and is entirely migratory. Most migrants would have left Miller's population very early in the breeding season; those few that pass even farther north than the central Washington population might possibly arrive somewhat later in the season. Another possible explanation of the invaders seen in the present study is that they were stragglers that tried unsuccessfully to establish territories farther south than the study area and then wandered northward seeking breeding space. In either case, the more northern population would have to deal with invaders later in the breeding season than would the California population. Begging and wing-fluttering in courtship feeding may appear only after the probability of the flutter display's being incited by invading migrants falls below some critical level; this level may occur earlier in the California population than in the Washington one.

SIMILARITY TO BEHAVIOR IN OTHER SPECIES

Aggressive displays.—Certain components of the flutter display are also found in agonistic displays of other passerine species. The horizontal position in particular is associated with aggressive displays in many species, e.g. Great Tit (Parus major) (Hinde, 1952; Jones, 1968); Varied Thrush (Ixoreus naevius) (Martin, 1970); Red-winged Blackbird (Agelius phoenicius) (Orians and Christman, 1968); and many species of Fringillidae; see for example Coutlee (1967) for American Goldfinch (Spinus tristis); Dilger (1960) for Common Redpoll (Acanthis flammea); and Dunham (1966) for Rose-breasted Grosbeak (Pheucticus ludovicianus). However in each of the above displays the head of the horizontal bird is directed typically toward its opponent, rather than away as in the flutter display.

A few passerines have agonistic displays in which the opponents do not face each other. The typical territorial boundary display in the Yellow-headed Blackbird (Xanthocephalus xanthocephalus) involves two males facing almost directly away from each other, with spread tail, drooped wings, and bill pointed down (Orians and Christman, 1968). The wings are not fluttered in this display. Stellar's Jay (Cyanocitta stelleri) has a display Brown (1964) called "aggressive sidling" in which the bodies of the opponents are parallel to one another, although the heads often point toward each other. Again the wings are not fluttered in this display.

Krieg (1971) described a remarkably similar display, called "wing-

flicking," in Eastern Bluebirds (*Sialia sialis*). Although the body is not horizontal, and the wings are sporadically flicked rather than steadily fluttered, the display is performed usually within 5 feet of the opponent, and the bird usually faces away from the opponent. It may be given by either sex, and could be elicited by introducing a live decoy into a pair's territory. Krieg (1971: 31) wrote that this display "appears to reflect a high attack tendency".

Sexual behavior.—Although it bears some resemblance to certain aggressive displays of other passerines, the flutter display of Loggerhead Shrikes probably bears more similarity to sexual displays of passerines than to any other behavior. This is particularly true of the wing-fluttering and begging notes. Hinde (1952) showed that both males and females of four species of titmice (Parus) fluttered their wings and gave begging notes in precopulatory displays. Hardy (1961) described similar behavior (crouch, wings fluttered, tail spread, begging notes) in the precopulatory display of the female Blue Jay (Cyanocitta cristata). Nice (1943) wrote that female Song Sparrows (Melospiza melodia) fluttered their wings when their mate approached right after their spring arrival on territory, and also in precopulatory display.

Cade (1962) wrote of the Northern Shrike: "there is a special, upright bill-raising display given by males and females—often during song—in which the wings are quivered, the tail is spread, and the bird's back is turned toward its mate" (p. 390). Cade considered the function of this display unclear and listed it under "courtship displays," yet he wrote that it occurred most often in response to the sudden close approach of another shrike. With the exception of the head position and the song, this display is remarkably similar to the flutter display of Loggerhead Shrikes. Further data, especially on the seasonal timing of this display, are needed before one can speculate on whether these two displays might be analogous.

Wemmer (1969) wrote of a display by Loggerhead Shrikes that he termed "displacement impaling" and interpreted as an "appeasement display," and which bears some resemblance to the flutter display. This included "lowering of the body to a near horizontal position, lateral orientation to the stimulus (e.g. human or other shrike), ruffling of the back feathers, and an upward lifting of the tail" (p. 213). Wemmer made no mention of any wing movements, nor did he report any calls associated with this display. Supposing this behavior to be the flutter display, it is not surprising that it was given in response to the presence of another shrike. At no time during the present study was the flutter display seen given in response to any stimulus other than the presence of another shrike.

Miller assumed that the display he saw on 30 November (see above) was sexual behavior. Yet he also wrote that he had never witnessed copulation in Loggerhead Shrikes. In the present study I recorded copulation by Loggerhead Shrikes a total of six times, involving four different pairs. In each case the only vocalizations were loud songs by the males, and although the male fed the female immediately before copulation in every case, neither bird fluttered its wings or gave anything resembling a begging note. The flutter display is indeed very similar to sexual behavior in other passerines; it may be that sexual behavior in Loggerhead Shrikes has become modified to avoid confusion with the flutter display.

EVOLUTION OF THE FLUTTER DISPLAY

Wing-fluttering associated with crouched posture also bears strong similarity to certain displays that several authors have termed "appeasement displays." These displays are usually associated with the beginning of courtship, and often are performed primarily by females. The term "appeasement display" should perhaps be restricted to behavior that may be performed by any subordinate bird, regardless of sex or time of year. Yet many investigators, e.g. Armstrong (1965: 265–266), Hardy (1961: 29), and Zahavi (1971: 204), have applied this term to displays by which a newly-arrived female announces her sex to a prospective mate.

It is true that the initial approach of two birds in a courtship situation may be very similar to an aggressive encounter. In species with little or no sexual dimorphism, a territorial male may determine the sex of a stranger entirely by its behavior. An intruding male will respond to a challenge either by returning the threat or by fleeing; a female will do neither, and yet will remain within the territory. In order to do so she must give a display that, among other things, serves to inhibit the attack of the male. It is the ability of this display to inhibit attack, regardless of the reason, that is of interest here.

A large body of literature supports the theory that threat displays of many avian species occur as a result of conflict between more than one type of behavior. Hinde (1952) described many instances of combination of elements in the behavior of Great Tits in the field. Marler (1956) demonstrated the importance of the balance between withdrawal and approach in the control of fighting in Chaffinches. Brown and Hunsperger (1963) strongly criticized this theory of conflicting tendencies on neurophysiological grounds. But the careful work of Jones (1968) with captive Great Tits showed that any time an attack stimulus was present, anything that prevented attack would evoke threat. It seems

likely that future work in the laboratory with captive birds of other species will provide further support for this theory.

Threat, then, is probably a result of simultaneous tendencies to attack and to do something else, such as flee. In territorial Loggerhead Shrikes this conflict might be particularly strong. Territorial invasion may provide the impulse to attack, but, as shown above, shrikes of the genus Lanius, possibly more than any other passerine genus, are capable of seriously injuring or even killing each other. This strong conflict has probably played a large part in the evolution of the flutter display. This display is given only when two rivals approach within a few feet of each other. At this distance the danger of being killed is very real. Possibly the wing-fluttering was originally associated with territorial encounters as an attack-inhibiting measure or "appeasement display." Later it became ritualized as a threat display, and hence no longer appears in its more usual role in mating, or even in courtship during the times when invasion is most likely.

SUMMARY

The flutter display of Loggerhead Shrikes is described. Data both from hand-reared birds in captivity and wild birds in the field indicate that this display functions in territorial defense, and may well indicate a high attack-tendency. The display preceded the only fight between wild birds seen in the study.

Although somewhat similar to agonistic displays of a few passerines, the flutter display bears strongest superficial resemblance to passerine sexual behavior. This is particularly true of the wing-fluttering and begging notes. In the study population, neither of these elements were seen associated with sexual behavior until well after the first broods had hatched. The period before hatching is when territorial invasion (and thus the flutter display) is most likely to occur.

The wing-fluttering and begging notes may originally (in evolutionary time) have acted as an attack-inhibiting display in aggressive situations. As shrikes are capable of inflicting serious injury to birds their own size with a single peck, selection for such inhibiting displays was probably strong. Later this behavior may have become ritualized as a threat display, and sexual behavior modified such that it bears least resemblance to the flutter display in periods when invasion is most likely to occur.

LITERATURE CITED

Armstrong, E. A. 1965. Bird display and behavior. New York, Dover Publ. Inc.

Bent, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U. S. Natl. Mus., Bull. 197.

- Brown, J. L. 1964. The integration of agonistic behavior in the Steller's Jay, Cyanocitta stelleri (Gmelin). Univ. California Publ. Zool., 60: 223-328.
- Brown, J. L., and R. W. Hunsperger. 1963. Neuroethology and the motivation of agonistic behavior. Anim. Behav., 11:439-448.
- CADE, T. J. 1962. Wing movements, hunting, and displays of the Northern Shrike. Wilson Bull., 74: 386-408.
- COUTLEE, E. L. 1967. Agonistic behavior in the American Goldfinch. Wilson Bull., 79: 89-109.
- DILGER, W. C. 1960. Agonistic and social behavior of captive redpolls. Wilson Bull., 72: 114-132.
- Dunham, D. W. 1966. Agonistic behavior in captive Rose-breasted Grosbeaks, *Pheucticus ludovicianus* (L.) Behaviour, 27: 160-173.
- Ellison, L. N. 1971. Spruce Grouse attacked by a Northern Shrike. Wilson Bull., 83: 99-100.
- HARDY, J. W. 1961. Studies in behavior and phylogeny of certain New World jays (Garrulinae). Univ. Kansas Sci. Bull., 42: 13-149.
- Hinde, R. A. 1952. The behaviour of the Great Tit (Parus major) and some other related species. Behaviour Suppl., 2: 1-201.
- JONES, N. G. B. 1968. Observations and experiments on causation of threat displays of the Great Tit (*Parus major*). Anim. Behav. Monogr., 1: 75– 158.
- KRIEG, D. C. 1971. The behavior patterns of the Eastern Bluebird (Sialia sialis). New York State Mus. Sci. Serv. Bull. No. 415.
- LORENZ, K. Z. 1952. King Solomon's ring. New York, Thomas Y. Crowell. LORENZ, K. Z. 1966. On aggression. London, Methuen.
- Marler, P. R. 1956. Behaviour of the Chaffinch, Fringilla coelebs. Behaviour Suppl., 5: 1-184.
- MARLER, P. R., AND W. J. HAMILTON, III. 1966. Mechanisms of animal behavior. New York, John Wiley & Sons.
- MARTIN, S. G. 1970. The agonistic behavior of Varied Thrushes (Ixoreus naevius) in winter assemblages. Condor, 72: 452-459.
- MILLER, A. H. 1931. Systematic revision and natural history of the American shrikes (*Lanius*). Univ. California Publ. Zool., 38: 11-242.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow, II. Trans. Linnaean Soc. New York, 6: 1-328.
- Orians, G. H., and G. M. Christman. 1968. A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds. Univ. California Publ. Zool., 84: 1–83.
- SMITH, S. M. 1973. A study of prey-attack behaviour in young Loggerhead Shrikes, *Lanius ludovicianus* L. Behaviour, in press.
- Wemmer, C. 1969. Impaling behaviour of the Loggerhead Shrike, *Lanius ludo-vicianus* Linnaeus. Z. Tierpsychol., 26: 208-224.
- ZAHAVI, A. 1971. The social behaviour of the White Wagtail Motacilla alba alba wintering in Israel. Ibis, 113: 203-211.
- Department of Zoology, University of Washington, Seattle, Washington 98105. Present address: Department of Biological Sciences, Wellesley College, Wellesley, Massachusetts 02181. Accepted 29 March 1972.