

0.01). Birds whose available foraging area was reduced by 50% increased the size of their territories to a greater degree than the other four groups ($P < 0.05$, nonparametric multiple comparison; Zar, *Biostatistical Analysis*, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1974). There was no significant difference in percent increase in territory size among the 0, 10, 20, and 30% groups.

After 10% of the available foraging area was made inaccessible to the birds in the nestling stage there was no significant change in territory size for either the male or female in the three pairs studied (Table 1). On average males increased their territories 1.4% ($N = 3$) and the females 7.1% ($N = 3$). Before manipulation average male territories ($\bar{x} \pm SD = 5220 \pm 1450 \text{ m}^2$, $N = 15$) were not statistically significantly larger than female territories ($\bar{x} \pm SD = 4460 \pm 1660 \text{ m}^2$, $N = 15$). In the pair studied during the fledgling stage there was a 6.1% decrease in the size of the male's territory and 57.1% increase in the size of the female's territory (Table 1).

Discussion.—Hinde (Behaviour Suppl. 2, 1952) found that when winters in England are unusually mild, Great Tits remain territorial; but if conditions become more severe, they form social groups. On warm days in late winter they will, at least temporarily, settle within their territories, possibly responding to the lowered energy requirements of mild days. Carpenter and MacMillen (Science 194:639–642, 1976) found that Hawaiian Honeycreepers (*Vestiaria coccinea*) shifted from territorial to non-territorial states in response to size of nectar supply and competitive pressure. Alterations of Rufous-sided Towhee territories were made when energy demands should be highest and response to limitation of food source should occur. Fluctuations in territory size from one stage in the breeding cycle to another are common in many species (e.g., Stefanski, Condor 69:259–267, 1967).

There have been few experimental, manipulative avian studies which attempt to determine if birds defend territories that supply more than minimal food resources. Featherstone (M.Sc. thesis, Univ. Toronto, Toronto, Ontario, 1966), using pesticides, decreased the foraging area of individual Ovenbirds (*Seiurus aurocapillus*) by 42% and found that the birds increased the size of their territories 38%. He concluded that the size of Ovenbird territories is at least partially determined by the amount of food present.

My results indicate that when 0, 10, 20, or 30% of the territories was made unavailable an adequate food supply was still available. Only when 50% of the territory was made unavailable was there a substantial increase in the territory size. There are at least two explanations for this result. One is that the function of territoriality is more than the procurement of a food resource. Territorial behavior in the Rufous-sided Towhee may also be a means of preventing sexual interference from conspecifics. An alternative, but not a mutually exclusive one, is that the birds are defending territories that contain more food than they can consume as insurance against a bad year.

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The shoulder-spot display in male Blue Grouse.—A “shoulder-spot” display has been described for both males and females of several species of grouse (Lumsden, Living Bird 9:65–74, 1970). The shoulder spot is formed by exposing the white underwing coverts at the proximal end of the humerus on the upper surface of the wing (Lumsden 1970). Movement of the patagial skin may also be important in effecting this display (Carbutt,

TABLE 1
 SEQUENTIAL ANALYSIS OF PRECEDING DISPLAY/FOLLOWING REACTION FOR INTERACTIONS
 BETWEEN YEARLING AND ADULT MALE BLUE GROUSE

Preceding display	Following reaction			
	Signaller		Receiver	
	Attack	Retreat	Attack	Retreat
Shoulder spot				
25	15	0	0	25

Wilson Bull. 93:98-99, 1981). This display in males has been associated with copulatory, ambivalent (or conflict), avoidance, and aggressive behaviors (Lumsden 1970; Hjorth, Vitrey 7:184-596, 1970; McNicholl, Ph.D. thesis, Univ. Alberta, Edmonton, Alberta, 1978; Garbutt 1981). However, descriptions of the display in the above studies have come primarily from observations of birds in unnatural situations such as disturbance by humans, interactions between birds in aviaries, encounters with mirror images during field studies, or responses to male and female dummies. Most reports lack description of the behavioral activities of the interacting birds before and after the display and also lack details of age and breeding status of the birds involved.

In 1980 and 1981, I recorded the movements and behavior of 24 yearling male Blue Grouse (*Dendragapus obscurus*) fitted with radio transmitters on Hardwicke Island, British Columbia. Age of birds was categorized as yearling (10-15 months of age) and adult (>15 months of age) based on the shape, color, and condition of the outer primaries (Braun, Outdoor Facts No. 86, Colorado Dept. Nat. Resour., 1971). Observations of birds were made with the aid of binoculars, using vegetation as natural blinds. If a bird was disturbed by my presence, details of activity were not recorded until he appeared to resume normal behavior such as feeding or preening. Radio transmitters appeared to have no effect on the behavior of birds. Observations were carried out from early April to mid-June in both years, and totalled 106 h.

Yearling males are rarely territorial. Rather, they associate with a few territories occupied by adult males (Jamieson and Zwickel, Auk 100:653-657, 1983). I observed yearling males interacting with territorial adult males 25 times. In each case, when the adult male detected a yearling on or near his territory, he immediately assumed a "feather spread" display posture (Stirling and Bendell, Syesis 3:161-171, 1970), then ran or flew toward the yearling. When 1-3 m from the yearling, the adult assumed a threat posture (McNicholl 1978) in which the feathers were laid flat against the body, the tail was lowered, the eye combs were red or orange, and white shoulder spots were visible. The adult quickly moved back and forth in front of and around the yearling, and on 11 occasions gave a "growl" (Stirling and Bendell 1970), an aggressive or threat call. When approached in this manner, yearlings invariably assumed a neutral posture (McNicholl 1978) and were never seen to display the shoulder spot during these encounters. On 10 occasions, the yearling remained in a neutral posture for 10-30 sec before flying from the area. In 14 other instances, the adult eventually rushed at the yearling and displaced him. I saw only one physical attack in which an adult pecked at the back of a yearling, removing several feathers.

On two occasions, two yearling males were seen to interact. In each case, both birds assumed threat postures with shoulder spots displayed before one displaced the other. I observed 11 instances of yearling males and 10 of territorial adult males courting females. I never saw shoulder spots in any of these cases.

Lumsden (1970) reported that male Blue Grouse display shoulder spots before and while attacking their images in a mirror. He concluded that the display may express fear in conflict with other behavioral states. McNicholl (1978) saw Blue Grouse displaying shoulder spots in various alert postures, at the approach of an observer while the male was courting a female, and during aggressive interactions. He suggested that the display represents fear, and perhaps subordination, in conflict situations. Hjorth (1970) observed shoulder spots on territorial Blue Grouse that were moving in the vicinity of an intruder. However, in summarizing the function of this display for grouse in general, he suggested that it is associated with subordination and avoidance behaviors.

It is sometimes difficult to interpret the signal content of a behavioral display. By using sequential analysis it may be possible to infer tendencies associated with given postures (Slater, pp. 131–153 in *Perspectives in Ethology*, Vol. 1, P. P. G. Bateson and P. H. Klopfer, eds., Plenum Press, New York, New York, 1973). For example, if the shoulder-spot display signalled fear or subordination, as some researchers have suggested, one would expect the signalling bird to retreat or act submissively after showing the display. Likewise, the receiver would not be expected to retreat or be attacked. Yet, Table 1 rather strongly implies that the shoulder-spot display signals aggression. This display was often followed by an attack by the signalling bird and invariably by the retreat of the receiver. Furthermore, the display was primarily given by territorial adult males when confronting non-territorial yearling males that had intruded on or near their territory. These observations suggest that under natural conditions the shoulder-spot display of male Blue Grouse is associated with aggressive behaviors and may function as a threat display. However, for other species of grouse this display may serve different functions. More observations of birds in natural situations are needed before further speculation on the evolutionary development of the shoulder-spot display and its role in the behaviors of various grouse species.

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Nestling growth relationships of Brown-headed Cowbirds and Dickcissels.—Data on nestling growth of brood parasites and their hosts are surprisingly few in the literature. Even the Brown-headed Cowbird (*Molothrus ater*), whose host relations have been studied in some other respects, has not been studied in any detail from this standpoint. This is particularly regrettable because the lack of host specialization and high incidence of multiple parasitism in this species recommend it for intensive studies of parasite-host growth relationships. Isolated or fragmentary records of growth in cowbirds are available in Friedman (The Cowbirds, C. C. Thomas, Springfield, Illinois, 1929), Pickwell (Trans. Acad. Sci. St. Louis 27:1–160, 1931), Herrick (Wild Birds at Home, Appleton-Century, New York, New York, 1935), Nice (Trans. Linn. Soc. N.Y. 4, 1937; Wilson Bull. 51:233–239, 1939), Mayfield (The Kirtland's Warbler, Cranbrook Inst. Sci., Illinois, 1960), and Nolan (Ornithol. Monogr. No. 26, 1978). Hann (Wilson Bull. 49:145–237, 1937) illustrated the growth of five cowbirds raised in three nests of the Ovenbird (*Seiurus aurocapillus*), Norris (Wilson Bull. 59:83–103, 1947) provided data for five individuals raised by different host species, and Scott (Wilson