AGGRESSION AND PLAY IN PENNED WHITE-TAILED BUCK FAWNS DURING WINTER

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ABSTRACT

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By

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The aggressive and play behaviors in a group of three buck fawns, Odocoileus virginianus, being fed ad libitum were compared to the behaviors of a trio given seven successive reductions in feed over a three month period of winter. The number of fights in the food-deprived group increased until food was reduced by 25.0 percent and then decreased. Fighting again increases as one fawn approached death from starvation. As compared to the control deer, when these fawns fought more, they tended to fight more intensely, play less, and fight almost exclusively over food.

Play and aggressive behaviors of the control trio were also compared to the behaviors of three fawns kept in a pen which was reduced in size seven successive times. Fighting increased until maximal levels of confinement, but then fawns became more tolerant of each other.

It was concluded that the number and intensity of fights, as well as the amount of play, were related to the availability of food and space. Additionally, the social relationships between fawns were adjusted to distribute stress unequally among group members. Hence, aggressive behavior is a significant parameter influencing survival at both individual and population levels.

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INTRODUCTION

White-tailed deer, Odocoileus virginianus, are stressed by shortages of food and space during winter. Bartlett (1950) estimated that the winter range of the Michigan white-tailed deer is 10-15 percent of the area of the summer range. This concentration of deer in specific habitat types often results in depletion of the winter food supply and in a significant number of deaths from starvation. Additionally, concentrating deer select wintering areas primarily on the basis of the cover value of the site and only secondarily on the amount of food present (Webb, 1948). As Allen (1948) summarized this phenomenon, "they keep coming back to the same swamp each winter until it's clean and then leave their bones among the cedars."

The social behaviors of wintering deer may be adjusted to meet the demands of these severe conditions. Intense social intolerance has been found in free-ranging deer during winter (Kabat, Collias and Guettinger, 1953) and in penned deer during winter (Robinson, 1962). Ozoga (1972) observed deer competing for food at white cedar (Thuja occidentalis) cuttings. He used the number of

conflicts per hour of observation as an index to the frequency of aggression and defined the intensity of aggression as the percentage of conflicts which were terminated by non-threat postures. Among deer feeding at these winter cuttings, he observed that the frequency of aggression increased while the intensity of conflict decreased from February to April.

The purpose of the present study was to determine how habitat features of spatial restriction and low food availability influence the change in play and aggressive behaviors over winter. The experimental null hypothesis was that changes in the amount of food or space would cause no changes in aggression or play. The philosophical hypothesis underlying this question is that severe winter conditions induce changes in social behavior which have survival value.

METHODS

Nine buck fawns, born and maintained in captivity, were weighed and grouped in three trios on October 25, 1972. Each trio was placed in a pen, 30 x 60 feet. Colored ear tags were attached to some deer, permitting visual recognition of individuals at a distance. A pre-treatment period of one month allowed the fawns to adjust to the new physical and social environment and to the presence of an observer during evening feedings. Eight treatment periods were scheduled, each 12 days long (Table 1).

Pen A was maintained as a control, with no alteration in food or space. Trio B was fed ad libitum but was kept in a pen which was reduced in size seven times. The rear wall of pen B was moved forward 5 feet at each 12-day interval, permitting gradual space reduction. Food was systematically reduced for the trio in pen C only. Food was reduced on the first day in each of periods 2-8 by the same percentages that space was reduced in pen B (Table 1). This reduction was based on the average daily amount of feed consumed by the control trio in pen A during the final

Table 1.--Treatment data for trios of male white-tailed deer fawns subjected to food or space shortages.

Treatment Period Number	Dates	Space Pen B (Square Feet)	Feed Pen C (gms./day)	Percentage Reduction
1	Nov. 30-Dec. 11	1800	4515*	0
2	Dec. 12-Dec. 23	1650	4240	8.3
3	Dec. 27-Jan. 7	1500	3867	16.7
4	Jan. 8-Jan. 19	1350	3246	25.0
5	Jan. 20-Jan. 31	1200	2800	33.3
6	Feb. 1-Feb. 12	1050	2263	41.6
7	Feb. 13-Feb. 25	900	2164	50.8
8	Feb. 26-Mar. 9	750	1227	58.3

*ad libitum.

six days of the preceeding treatment period. Commercial deer feed (Andersons'--Maumee, Ohio) was used.

Behavioral patterns of each trio were observed for 30 minutes a day from behind a 4 x 8 feet canvas shield which had a small rectangle cut out to permit viewing. A measured amount of feed was introduced to the group at the zero minute of observation. Observations of trios were made on a rotating schedule to reduce differences due to the order of observation or time of day. Observation periods were adjusted during winter so that observation of the last group ended approximately a half-hour before sunset. Food was left in the pen until observation-time

the following day, when any remaining feed was removed and weighed.

Aggressive and play interactions between fawns were recorded for each observation period. Aggression occurred over food, bedding places and right-of-way when moving. Some encounters were observed in which the releaser for aggression could not be objectively defined; these were lumped as "other" aggressive interactions. The aggressive postures, which comprised components of a sequence, were classified according to descriptions given by Thomas, Robinson and Marburger (1965). These authors described aggressive display as a series of postures arranged in a sequence of increasing intensity. If an opponent duplicated the posture was displayed by the aggressor until the withdrawal of one deer terminated the sequence. The fawn sequence in order of increasing intensity was "ear drop," "hard look," "sidle," "strike," and "flail." Ear drop, hard look and sidle were used as threats; strike and flail involved contact by kicking with the forefeet.

The following characteristics of play were used to differentiate play (including aggressive play) from aggression:

1. Play elements are derived from other contexts such as fighting, courtship, or escape situations (Ewer, 1968).

2. Elements of play usually do not follow each other in any fixed order or sequence (Leyhausen, 1965).

3. Behaviors used in play may appear more exaggerated and displayed with more exuberance than the situation requires (Leyhausen, 1965).

4. Play usually occurs at specific times in the daily activity cycle (Meyer-Holzapfel, 1956).

5. Play occurs only at times when no instinctive pattern is activated (Meyer-Holzapfel, 1956).

6. Dominance relationships may be reversed during play (Ewer, 1968).

RESULTS

Control Trio

The control trio was watched for 30 minutes a day for 96 days, during which time the number of aggressive conflicts was recorded (Table 2). The mean number of fights per hour of observation was calculated for each 12-day treatment period.

Conflicts over food accounted for 67.3 percent of the encounters. Fighting over food gradually decreased from 4.8 conflicts per hour of observation during period one to 0.8 per hour in period 4. As winter progressed, fighting gradually increased to 3.2 encounters per hour in the final period. The number of aggressive displays unrelated to food varied from period to period with no apparent pattern.

The intensity of aggression was defined as the percentage of conflict which was terminated by contact displays. Intensity of conflict (Table 3) in the control group tended to increase until period 6. It then decreased sharply in the last two weeks.

The relationship between the amount and severity of fighting during treatment periods was tested by applying

Table 2.--Mean numbers of aggressive encounters per hour of observation during successive 12-day periods.

Treatment Period	Encounters Over Food			Other Aggressions		
	Trio A	Trio B	Trio C	Trio A	Trio B	Trio C
1	4.8	1.3	2.0	0.7	0.0	1.2
2	1.8	1.5	2.2	0.3	0.3	0.5
3	2.7	3.5	5.7	1.8	2.3	0.5
4	0.8	1.7	5.7	1.2	0.3	0.8
5	1.2	2.8	3.0	2.3	2.3	0.8
6	1.2	2.7	1.8	0.7	3.7	0.7
7	1.5	0.8	11.0	0.5	4.7	0.5
8	3.2	2.0	12.0	0.8	0.8	0.0

Table 3.--Intensities of aggressive encounters: Percentages of encounters terminated by non-threat displays.

Treatment Period	Control Trio A	Space-Limited Trio B	Food-Limited Trio C
1	58	50	53
2	62	91	62
3	52	80	92
4	67	92	80
5	67	74	88
6	73	55	64
7	58	58	86
8	50	65	95

the Spearman rank correlation coefficient. The intensity and frequency of aggression were negatively correlated ($n=8$; $r_s=-0.74$; $p<0.025$). When the control group fought more, the conflicts tended to be less severe.

Play encounters (Table 4) most often occurred toward the end of the 30-minute observation intervals. Aggressive play, or "mock fighting," was evident in 58.7 percent of the play encounters. No relationship was found between the amounts of aggressive and non-aggressive play observed ($r_s=-0.02$; $p>0.10$). However, the amount of aggression was positively correlated with both aggressive play ($r_s=0.75$; $p<0.05$) and total play ($r_s=0.76$; $p<0.025$).

Space-Limited Trio

Fighting over food among fawns in the space-reduced pen increased slightly during the study from 1.3 to 2.0 conflicts per hour of observation (Table 2). However, a lower percentage of the total fighting was related to food (52.4%), compared to the control trio (67.3%). The dominant fawn would frequently attack the two subordinates for no apparent reason. During periods 7 and 8, when spatial restriction was greatest, these fawns displayed less total aggression than they did during periods 5 and 6.

Intensity of aggression varied between treatment periods but, unlike the control trio, the space-limited group used more intense displays at the end of the study than at the beginning (Table 3).

Table 4.--Mean number of play encounters per hour of observation during successive 12-day periods.

Treatment Period	Aggressive Play			Non-Aggressive Play		
	A	B	C	A	B	C
1	9.3	2.1	4.1	2.6	1.3	1.3
2	6.0	4.1	0.6	3.5	1.3	0.1
3	3.3	3.0	0.1	6.0	1.5	0.6
4	5.3	1.3	0.1	3.6	2.3	0.0
5	8.6	1.5	0.0	5.6	1.1	0.5
6	3.3	0.6	0.3	1.5	0.5	1.3
7	3.1	0.8	0.0	3.6	1.8	0.1
8	5.8	0.0	0.0	5.0	0.1	0.0

The space-limited group played less than the control group (Table 4) and also played less during period one before the pen was reduced in size. Despite this initial difference between groups, play decreased at a greater rate in trio B than in control trio A. Furthermore, aggressive play decreased at a faster rate than non-aggressive play.

Food-Limited Trio

Fighting for food increased (Table 2) until the fourth period when a 25.0 percentage reduction in feed was realized. Fighting then decreased until the level of reduction reached 50.8 percent when the number of

encounters increased sharply. In order to explain this bimodal distribution (Fig. 1), the change in relationship between fawns was examined. The majority of aggression in all trios was seen between the fawns of dominance rank 1 and rank 2. Conflict between the dominant rank 1 and the most subordinate rank 3 was also significant. Very little fighting was observed between ranks 2 and 3 in either the control or space-limited groups, yet fighting between ranks 2 and 3 in the food-limited group was pronounced. Change in the rate of fighting between these two fawns (Table 5) accounted for most of the initial increase and progressive decrease in group aggression for the trio.

Initially the food-limited group either fed together or took turns at the feeder. As food was reduced, all three fawns began to increase fighting. At 25.0 percentage reduction the dominant fawn began to keep the rank 2 deer away from the feeder, but the dominant and rank 3 fawns fed together. As a result of this change in social organization at the feeder, fighting between 1 and 3 dropped since the dominant appeared to become more tolerant of the subordinate. Fighting between rank 2 and 3 fawns was reduced while the dominant kept the rank 2 deer from the feeder and hence decreased the opportunity for 2 and 3 to interact. At the maximum reduction of food, during periods 7 and 8, the social structure at the feeder again changed and the dominant also began to keep the rank 3 deer from the feeder for the first 10-15 minutes of the

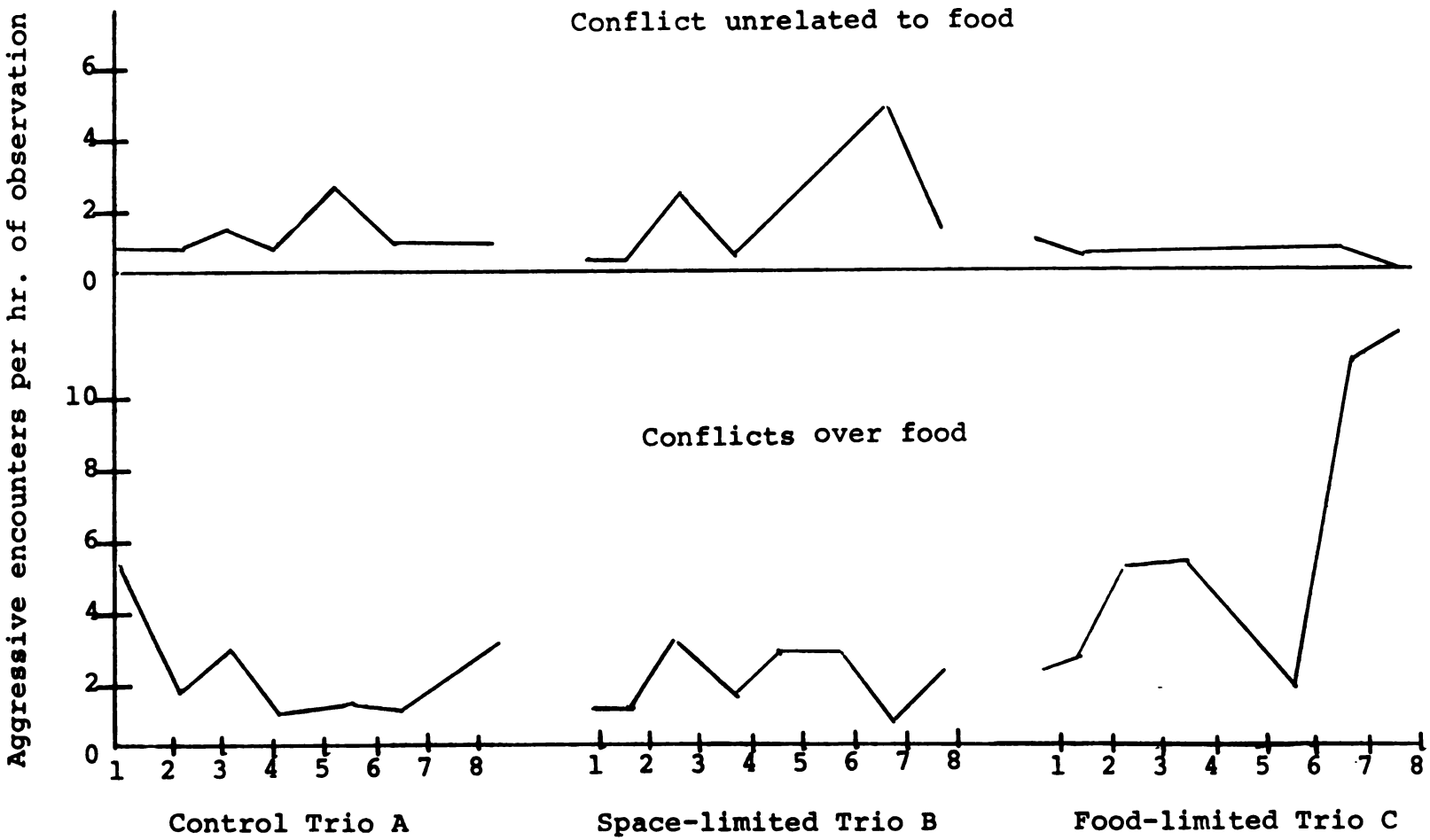

Figure 1. Mean number of aggressive encounters per hour of observation during successive 12-day periods.

Table 5.--Mean number of aggressive encounters over food between pairs of individuals per hour of observation.

Treatment Periods	Trio A			Trio B			Trio C		
	Individuals								
	1&2	1&3	2&3	1&2	1&3	2&3	1&2	1&3	2&3
1	3.0	1.3	0.5	0.1	0.8	0.3	0.8	0.1	1.0
2	1.0	0.5	0.1	0.8	0.6	0.0	0.3	0.6	1.1
3	1.1	1.1	0.3	2.0	1.3	0.1	2.1	1.3	2.1
4	0.5	0.1	0.1	0.6	1.0	0.0	1.5	2.8	1.3
5	0.8	0.1	0.1	2.0	0.6	0.1	1.5	0.8	0.6
6	0.5	0.3	0.3	1.3	1.1	0.0	0.8	0.8	0.0
7	0.8	0.6	0.0	0.3	0.5	0.0	6.1	3.8	1.0
8	2.1	0.8	0.1	1.8	0.0	0.1	7.0	4.1	0.8

observation interval. The rank 2 deer no longer passively waited but made continuous attempts to gain access to the feeder. The number of encounters between all fawns increased.

Aggression also became more intense as food was reduced (Table 3). The minimum intensity occurred during period one, before the amount of feed given the trio was reduced. Maximum intensity occurred during period eight when the least amount of food was offered. For this trio, when aggression was frequent, it also tended to be intense (r_2=0.70; $p<0.05$).

The amount of both aggressive and non-aggressive play decreased suddenly after the first reduction in feed (Table 4). Aggressive play was reduced more than non-aggressive play.

Aggressive, Submissive and Play Postures

Ear drop, hard look and sidle were used as threats. Although ear drop was displayed as an independent posture, it occurred more often in combination with the sidle or hard look. "Lip curl," the retraction of both upper and lower lips, was observed on rare occasions in association with ear drop (Fig. 2).

Contact aggression included hair biting and pulling, and the strike. Several distinct forms of the strike were displayed. In some strikes, contact was made during an upward sweep of the forefoot (Fig. 3). In others, the

Figure 2. Lip curl was seen in some aggressive encounters.

Figure 3. Some strikes occurred in which contact with the opponent was made during an upward sweep of the forefoot.

sharp edges of the hoof made contact with the opponent on a downward sweep of the forefoot. Series of successive striked were observed on a few occasions. The same forefoot was used if the aggressor was stationary but alternate forefeet were used to strike a fawn which was being chased from the feeder. The most intense strikes occurred when the deer used both forefeet simultaneously. The flail, where deer stand upright and strike with both forefeet, was never observed. Threat did not precede all strikes. Sometimes when fawns were in close proximity to each other strikes were delivered without warning.

Appeasement behaviors were displayed in all trios but were most pronounced in the space-limited group where withdrawal from an aggressive encounter was inhibited by the size of the enclosure. The "crouch" was displayed with the neck extended and pointed down. A "head bob" was displayed by twisting the head to the side away from the opponent and moving it up and down. This posture usually changed an aggressive encounter into a play encounter. Additionally, fawns often licked the tarsal gland of a deer at the feeder and then were granted access to the food without encountering an aggressive display.

In order to differentiate true aggression from aggressive play, it was necessary to evaluate the postures used during play. All aggressive postures previously discussed were observed during play, often without being

displayed in any sequence of intensity. The rush (Fig. 4), an adult-buck aggressive display, was only observed during play. "Driving," an adult-buck courtship display (Pruitt, 1954), was observed in play encounters. Driving superficially resembled the hard look but was displayed with a swinging gait and emphatic stomping of the forefeet while running towards the play mate (Fig. 5). "Gamboling" (Espmark, 1969), or energetic jumping into the air, was rare (Fig. 6).

Figure 4. The rush, an adult buck aggressive posture, was displayed by fawns only during play.

Figure 5. Driving, an adult buck courtship posture, was displayed by fawns only during play.

Figure 6. Gamboling appeared to be the only play posture not used in any other biological context.

DISCUSSION

Control Trio

It was anticipated that the pre-treatment period would limit the high frequencies of aggression often found in newly-formed social groups when dominance heirarchies are first being established. However, aggression in the control trio still decreased over winter. This may have occurred from continuing definition of the dominance heirarchy as fawns matured and gained experience interacting with other group members. The decrease in aggression may also have reflected a seasonal decrease in activity. Food consumption (French et al., 1955), metabolism (Hoffman and Robinson, 1966) and activity (Ozoga and Verme, 1970) of deer have been found to decrease during winter and increase in spring. The curve for frequency of aggression over food (Fig. 1) in this group also decreased during winter and increased slightly at the end of winter.

Towards the end of the study the control group used more threat and less contact aggression during encounters. This might be expected in groups of maturing juveniles who become more adept in the use of socialized displays. A

threat from a fawn of known dominance may have become more efficient in inducing withdrawal in a subordinate as the fawns become more experienced with one another and learned their position in the dominance heirarchy.

Space-Limited Trio

The increase in fighting unrelated to food was primarily due to the flagrant hostility of the dominant fawn. However, as space was still further reduced, aggression decreased. This inhibition of aggression during extreme restriction of range suggests that deer at especially high densities may not be overly intolerant if sufficient food is present.

The rise in intensity of conflict among members of this trio may have resulted from the inability of a fawn to completely withdraw after having been defeated in an encounter. Despite the subordinate fawn's attempt to escape, the mere presence of the defeated fawn may have elicited more intense threats from the dominant animal.

Play decreased in this trio, as compared with the control group. Since play in young ungulates centers around flight or escape (Meyer-Holzapfel, 1956), and since flight and escape were restricted as the pen was reduced in size, play may have been inhibited. Additionally, the subordinates may have refrained from using play postures in order to prevent a play encounter from releasing aggression in the dominant fawn. The finding that

aggressive play was reduced more than other forms of play as pen size was decreased gives further support to this idea.

Food-Limited Trio

Fighting increased with initial food deprivation and then decreased between 25.0 and 50.8 percent feed reduction. Southwick (1967) found that rhesus monkeys (Macaca mulatta) showed a similiar increase and decrease in fighting with progressively greater food shortages. He attributed the decrease to fatigue and lethargy resulting from malnutrition. In the present study, the decrease in aggression occurred with a change in social organization of deer at the feeder.

At levels of extreme food deprivation during periods 7 and 8, fighting again increased. The rank 2 fawn nearly died from starvation as it lost 22 percent of its maximum body weight (Table 6). As survival of this fawn was threatened, aggression showed a maximum increase.

Robinson (1962) subjected 15 fawns to food deprivation in order to determine the relationships between condition and social rank. Three of the deer died from starvation, but none of these deer was the most subordinate. Similarly in the present study, the rank 2 lost more weight and was nearer death than the rank 3 fawn. Survival in deer experiencing winter food shortages might be

Table 6.--Weight changes of individuals and groups as a function of time, treatment, and social rank.

Trio	Deer No.	Social Rank	Pounds						% Weight Change
			10/24	11/30	12/27	1/9	2/14	3/10	
A	759	1	83	92	93	92	99	100	+20
	710	2	100	111	113	109	115	109	+ 9
	754	3	73	87	86	82	89	89	+22
B	716	1	89	97	105	96	102	102	+15
	728	2	63	71	75	70	73	62	- 2
	773	3	72	81	79	79	82	76	+ 5
C	755	1	87	98	98	96	98	90	+ 3
	785	2	86	83	96	93	92	75	-13
	746	3	71	82	84	79	78	66	- 7
A*			85	97	97	94	101	97	+17
B*			75	83	86	82	86	80	+ 7
C*			81	88	93	89	89	77	- 5

*Trio means.

expected to be highest for those population segments with either the most aggressive or least aggressive deer.

Intensity of aggression in this group also increased over winter. The increase in the number of attempts of the subordinates to approach the feeder or to refuse withdrawing from the feeder required the display of more intense postures. Food deprivation has been shown to lower the threshold for withdrawal responses (Hall, 1941).

Altmann (1952) found that elk (Cervus canadensis) played less on a poor summer range than on a range with adequate food and cover. The present study experimentally verified that deer play less at very low levels of nutrition. The space-reduced group also played less than the controls, hence play seems to be not only related to food but appears also to be a sign of general well-being in fawns.

Aggressive, Submissive and Play Postures

Thomas et al. (1965) found that buck fawns displayed the aggressive patterns characteristic of adult does. The fawns in the present study did display the rush, an adult buck aggressive display, but only in play encounters. They frequently butted the chest, forelegs and flanks of an opponent which would be maladaptive for adult bucks with antlers. The function of aggressive display is to determine priority for distributing resources

among group members without inflicting injury or wasting energy. Ritualization and socialization of display minimizes violent contact and thereby reduces the chance of a male killing his own offspring (Ewer, 1968). It follows that the buck fawns were learning how to rush. Butting of the flank and chest may be an immature form of the rush.

A separate study was undertaken to document and investigate the phenomena of hair-pulling and hair-loss. For the purpose of the present study, hair-pulling was considered to be an aggressive behavior when it elicited aggressive display or withdrawal in a competitive situation.

Strikes delivered without threat have been reported by Thomas, Robinson and Marburger (1965), who stated that the orderly sequence of display sharing did not always occur. They found that a less intense posture never followed a more intense display. Observations during the present study indicate that the probability of one display following another is not only dependent on the intensity of the conflict, but also upon the distance between deer at the onset of the encounter. Since white-tailed deer have no fixed geographic territory, the portable territory around each animal becomes critical, as does the distance at which other deer are permitted to approach with given visual displays.

The literature on social strife in the white-tailed deer has concentrated on aggressive display with less

consideration given to submissive or appeasement postures. One function of socialized display in the Cervidae is to allow defeated individuals to remain in the herd, thereby maintaining group cohesion. Submissive and appeasement behavior may be significant in reducing overt aggression which disrupts cohesion. In the fallow deer, Dama dama, the submissive posture of lowering the neck has been described (Burckhardt, 1958) and assumed to be derived from the attitude of the young when approaching to nurse. Too few observations were made in the present study to permit an analysis of submissive behavior other than to report its occurrence, although its role in species survival may be important.

Play postures were shown to be a mixture of displays from fighting, escape and courtship sequences. Adult displays, present in varying stages of development, were shown in fawn play. Gamboling appeared to be the single posture in the fawns which was specific only to play.

CONCLUSION

Penned buck fawns expressed considerable social strife over food, even in a control group given surplus feed. These six-month old fawns were adept at expressing aggression using a complex system of visual displays.

The number and intensity of fights, as well as the amount of play, were related to the availability of food and space. Fawn groups were able to modify aggression and play to meet the demands of food and space shortage. Hence, the null hypothesis of equal change in play and aggression between the three trios was rejected.

The social organization of these fawns was also adjusted to distribute stress among group members. Hence aggressive behavior does not only have individual survival value but may function at a population level to minimize winter mortality.

Natural selection for deer most capable of expressing submission as well as those most capable of expressing dominance may have a stabilizing effect on deer populations subjected to annual periods of stress and mortality. This mechanism may prohibit the evolution of

a deer society composed entirely of aggressive animals capable of surviving hardship but ultimately selected to destroy one another.

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