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THE RELATION OF STATUS TO BEHAVIOR AND ANATOMY IN DOMINANCE HIERARCHIES OF SIX-LINED RACERUNNER LIZARDS

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THE RELATION OF STATUS TO BEHAVIOR AND ANATOMY IN DOMINANCE HIERARCHIES OF SIX-LINED RACERUNNER LIZARDS

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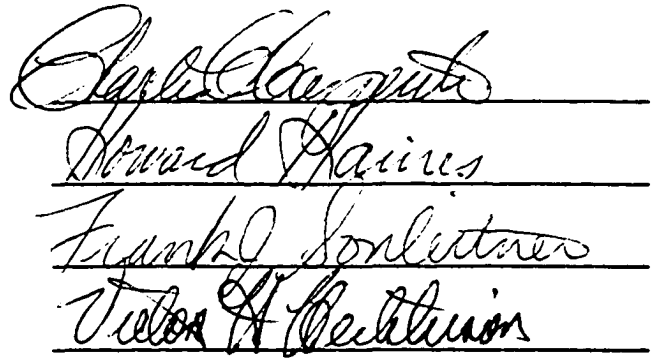

DISSERTATION COMMITTEE

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THE RELATION OF STATUS TO BEHAVIOR AND ANATOMY IN DOMINANCE HIERARCHIES OF SIX-LINED RACERUNNER LIZARDS

Abstract

Captive six-lined racerunner lizards readily establish linear dominance hierarchies during the breeding season. Dominance is established via frequent aggressive interactions. Trios of males were observed to determine the relation of status to behavior and anatomical state. Individual rank was closely related to body weight. Dominant males were most active and were aggressive throughout the breeding season. Intermediate and low rank males rarely exhibited aggesssive behavior. Dominant males, unlike lowest ranking males, readily attempted to mate with females. Anatomical comparisons showed such behavioral differences to be related to testicular state. Feeding behavior and nutritive state were not related to social rank. Stress, measured by adrenal size, was related to status. Aggression of dominant males may account for adrenal hypertrophy among subordinates. Dominant males exhibited the greatest frequency of occurrence of tail autotomy, a measure of precapture susceptibility to predation.

Introduction

The six-lined racerunner, Cnemidophorus sexlineatus, readily establishes dominance hierarchies in captivity (Carpenter, 1960; Hardy, 1962; Fitch, 1958). Male lizards are dominant over females, although exceptions occur, with large females occasionally dominating small males (Hardy, 1962; Carpenter, 1960).

The aggressive interactions which maintain dominance hierarchies among captives have also been described for wild populations. Six-lined racerunners are a nonterritorial species and forage over large ranges, with individual isolation maintained by mutual intolerance (Carpenter, 1962). In a typical encounter, subordinate animals flee, or are chased by dominants. Thus dominance relationships among captives are representative of the social dynamics of wild populations.

Hierarchy organization and aggressive behavior have been adequately described for these lizards. However, as with studies of hierarchies for other species, the factors which determine individual status, such as age, sex, and experience, and the effects of status on individual fitness are not understood. This study was designed to determine how dominant and subordinate animals differ and to relate differences in behavior to anatomical indices of physiological state.

The sexual behavior of a male is related to its status

in a hierarchy (Hardy, 1962; Carpenter, 1960). However, little is known of the relation of status to testicular state. This, and the possible effect of status on breeding condition, were investigated.

Dominant male racerunners feed more readily in captivity and inhibit feeding by subordinates (Hardy, 1962). Thus, differences in feeding behavior and the effects of status on nutritive state, measured by stomach content, lipid and glycogen deposition, and weight change are analyzed.

Many investigators have attempted to measure the stress a subordinate animal undergoes, when subjected to agression by conspecifics. Archer (1970) showed that agression induces adrenal hypertrophy in subordinate mice. Christian (1963) cites a number of studies which showed that adrenal hypertrophy in subordinate mammals results from density-induced stress. This has also been confirmed in avian hierarchies (Siegel and Siegel, 1961) and sunfish (Erickson, 1967). Although adrenal hypertrophy in response to intraspecific aggression has not been directly confirmed in reptiles, seasonal adrenal hypertrophy of some species coincides with the period of peak intraspecific aggression (Lofts, et al., 1971; Wilhoft, 1964). Therefore, adrenal volumes were selected for comparison of stress between various ranks.

Six-lined racerunners are able to autotomize a tail segment when seized by a predator. Autotomy infrequently results from intraspecific aggressive interactions (Carpenter, 1960).

The tail regenerates rapidly, but the altered pattern of scalation which results allows ready determination of precapture autotomy. The frequency of occurrence of precapture autotomy was compared for dominant and subordinate animals.

Methods

Lizards were collected and observed from 1972-1975, during the summer breeding season. A total of 48 groups of lizards were observed in outdoor arenas located at the behavior laboratories of the Oklahoma University Biological Station and the University of Oklahoma Norman campus.

Each arena was enclosed by galvanized metal walls, 15 feet x 15 feet x three feet high, covered by chicken wire mesh to prevent predation by birds.

The arena habitat consisted of loose, sandy soil, partially vegetated to allow cover for insect prey. Concrete blocks were provided as cover and crawlways for foraging lizards. Mealworms and captured insects supplemented their diet, and vegetation was watered daily.

The racerunners were live-trapped in the vicinity of the behavior laboratories. Upon capture, lizards were immediately weighed to the nearest 0.1 gram, color-marked and toe-clipped for individual recognition and placed in arenas. Each arena contained three males. All males were adult or near adult. Individual females were also placed with each group to determine the sexual responses of males.

Methods of Observation

Observations commenced within twelve hours of capture and continued until a group was removed, so that changes in

hierarchal structure or individual rank could be noted. Most observations occurred from 0900 to 1200 hours, during the peak of the daily activity cycle (Carpenter, 1960).

The rank of each male was determined by the outcome of male-male encounters, the most aggressive animal classed as rank 1, intermediates as rank 2, and the subordinates of a trio classed as rank 3. Individual behaviors were classified as aggressive or submissive. Behaviors not associated with male-male interactions were also recorded and classified.

Behavior Classification

The acts which males performed were categorized according to the context in which they occurred. The following is a description of each category and its components:

a) avoidance behavior: acts in which a male avoids contact with another male. Responses observed include evasion, in which a lizard moves slowly away from another; flight, in which a male runs to avoid contact; and freezing, whereby a subordinate remains motionless to avoid detection by a dominant.

b) aggressive behavior: acts performed following visual contact directed toward a subordinate lizard, including approach, in which a male moves toward another animal following visual contact; chasing, in which a male pursues a subordinate; biting, whereby a male grasps a subordinate's tail; and head bobbing, a behavior observed following an encounter with a

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subordinate.

c) mating behavior: behaviors which result in, or arise from, contact with a female; approach, chase and biting behaviors, similar to aggressive behaviors are herein included. Since sexes exhibit distinct color dimorphism, and female avoidance behavior is distinctive (Carpenter, 1960), it is assumed that such behaviors toward females imply sex recognition and warrant separate classification. Other behaviors in this category include search, a male behavior observed following contact with a female, involving rapid searching movements in the direction of female flight; mating, involving copulation attempts during contact; and femoral rubbing, rapid rubbing of the femoral region against the substrate or the body of a female during copulation.

d) thermoregulatory behavior: comprising behaviors related to the activity level of a lizard. This includes basking, in which a lizard lies motionless with legs spread for maximal absorption of radiant energy; and burrow entering, followed by emergence after a brief period.

e) feeding behavior: including foraging, a search behavior characterized by digging, overturning debris with the snout, and pursuit of moving insects; and feeding.

Analysis of Anatomical Variation

After observing each group for one to two weeks, the lizards were removed, immediately killed, and reweighed. Each animal was examined for evidence of autotomy and injury. The testes and epididymus, liver, stomach with contents and abdominal fat bodies were removed and weighed to the nearest milligram. Adrenal glands were removed and their volumes measured with an ocular micrometer. Body snout-vent length was also determined.

The paired testes and epididymi of each lizard were fixed in calcium formal. One of each was routinely paraffin-embedded, sectioned at 7 , and stained with hematoxylin. Testes sections were examined for sperm presence. Average seminiferous tubule diameters were determined with an ocular micrometer to serve as quantitative indices of testicular activity. Epididymus sections were examined for the presence of sperm.

Control animals were killed and examined upon capture to provide anatomical comparisons with captives.

Student's t-test was used to compare means in statistical analyses. Percentages were compared by the arcsine transformation (Sokal and Rohlf, 1969).

Results

Seasonal Changes in Social Organization

Captives observed in early May did not show dominant behavior. Males readily foraged and fed, and rapidly adjusted to captivity. When two males met, both would turn away, avoiding contact. Occasionally, one would freeze until the other moved out of sight, or flee, but such incidents were rare. Of 42 encounters recorded from 3 May to 12 May, no aggressive behavior was observed.

The earliest such incident was recorded 19 May. Of 18 encounters observed 23 May, three resulted in pursuit by a large male. During the remaining encounters, males fled but were not approached or pursued. By 1 June, large males readily pursued small males and dominance hierarchies were established.

A number of features characterized these hierarchies:

1) linearity: Of 40 groups which maintained hierarchies, none exhibited variable dominance relationships. High-ranking males always dominated low-ranking ones and encounters always resulted in submissive behavior by the latter.
2) stability: Hierarchies remained established throughout the study periods (2 weeks for each group). Exceptions occurred at the end of the breeding season,

in late July. At this time, a number of groups established hierarchies when first placed in captivity, but dominance relations disappeared by 1 August.

3) fixed status: No male, after attaining a specific rank, later changed status. Dominance shifts only occurred when a male was removed from the arena, or when a stranger was introduced. As an example of a shift in rank, a low ranking male was left in an arena after the other members of its group had been removed. When two new males were introduced, the former resident became the dominant animal in the new group.

4) rapidity of hierarchy formation: When a group is introduced to an arena, the hierarchy is rapidly established. In all instances, the hierarchy was stable by the first observation period, i.e., within 12 hours after the group had been introduced. In one instance, a stable hierarchy was established within 10 minutes. This was due to the presence of a very aggressive, active dominant male which rapidly encountered the other group members.

5) active aggression: Although some encounters did not result in aggressive interactions, hierarchies are maintained by encounters in which dominant males frequently pursue, and occasionally bite subordinates.

6) male dominance: Although low ranking males sometimes fled females near the end of the breeding season, females do not pursue or approach males during the breeding season. Females do not exhibit aggressive behavior and only influence encounters passively.

From June to 1 August, hierarchies characterized by the preceding list of attributes were observed among captives. During the last week of July, pronounced changes occurred in the patterns of male interactions. Hierarchies were not apparent. Males could no longer be assigned a rank because of the variability of their response to encounters. Contact often resulted in mutual avoidance. Sometimes one male would flee but there was never any indication of overt aggression.

During the breeding season, females did not elicit submissive behavior from adult males. By August, however, large males avoided and occasionally fled females.

Relation of Status to Activity and Behavior

Racerunner lizards remain in burrows when inactive. The order of emergence of group members, at the onset of the morning activity period, was determined, to show the relation of emergence to rank (Table I). Dominant males always emerged after subordinates and females. In only one instance did a rank 2 male emerge first. The frequency of first emergence of rank 3 males and females was significantly greater ($p < 0.002$, Fisher's Exact Test).

The duration of daily activity was not quantified. Instead, the relation of status to number of acts observed was determined by summing the individual acts attributed to members of each group (Table II). Although rank 1 males emerged later than subordinates, they performed 50% of all acts recorded, a significantly greater contribution than ranks 2 and 3 ($p < 0.001$). Dominant males were also involved in significantly more encounters than were other males ($p < 0.01$ Table III).

Encounters were analyzed to determine which ranks interacted most frequently. Interactions between ranks 1 and 2 accounted for 48% of all encounters, while 20% involved ranks 2 and 3, a significant difference ($p < 0.05$).

Table IV lists the number and percentage of aggressive interactions resulting from encounters between various pairs. Encounters between rank 1 and 2 males account for 70% of all aggressive interactions observed, significantly more than the 18% resulting from interactions between ranks 1 and 3 ($p < .02$).

The frequency of acts for the various behavior categories was tabluated for each rank (Table V). Avoidance behavior was exhibited almost exclusively by subdominant males and females. Only once did a rank 1 male flee a subordinate. Rank 2 males exhibited 62% of all avoidance behaviors observed due to frequent encounters with rank 1 males. The lowest ranking males, and females, contributed equally to the total observed avoidance behavior. Both were less active, thus

Table I. Relationship Between Social Rank and the Order of Daily Emergence; listed as the number of times each rank was first to emerge.

Social Rank	No. of times of first emergence	%
1	0	0.0
2	1	7.7
3	6	46.2
Females	6	46.2

Results based on 13 observation periods on six groups.

Table II. Number of Behaviors for Each Rank and % of total Observed Behaviors Attributed to each Rank.

Social Rank	No. of behaviors observed	% of total behaviors attributed to each rank
1	276	50.1
2	189	34.4
3	85	15.5
Total	550	100.0

Results from 42 observation periods on 24 groups.

Table III. Number of Male-Male Encounters Observed for Each Rank and % of Total Observed Encounters Attributed to Each Rank.

Social Rank	No. of encounters observed	% of total encounters attributed to each rank
1	118	43.3
2	99	36.4
3	55	20.3
Total	272	100.0

Results from 42 observation periods on 24 groups.

Table IV. Aggressive Interactions Resulting from Encounters Between Various Pairs of Ranks.

Rank pair	No. of aggressive interactions	% of total
1 vs. 2	34	70.8
1 vs. 3	9	18.8
2 vs. 3	5	10.4
Total	48	100.0

Results based on 24 observation periods on 10 groups.

Table V. Number of Acts of Five Behavior Categories Recorded for Each Rank and Females, and % of Total Acts Attributed to Each Rank.

Behavior category	No. and % of total observed behaviors attributed to ranks and females				
	Rank				
	1	2	3	Females	Total
Avoidance:					
N	3	62	36	41	142
Percentage	2.1	43.7	25.4	28.8	100.0
Aggression:					
N	100	10	6	1	117
Percentage	85.5	8.5	5.1	0.9	100.0
Mating:					
N	84	42	8	1	135
Percentage	62.3	31.1	5.9	0.7	100.0
Thermoregulation:					
N	16	10	7	5	38
Percentage	42.1	26.3	18.4	13.2	100.0
Feeding:					
N	24	13	6	10	53
Percentage	45.3	24.5	11.3	18.9	100.0

Results based on 24 observation periods on six groups.

encountering higher ranking males less frequently than rank 2 males.

Rank 1 males exhibited 85% of all male-directed aggression, including approach and chase, biting and head bobbing (Table V). Rank 1 males chased subordinates in 59% of their encounters, whereas rank 2 males rarely chased subordinate males and exhibited only 10% as many aggressive acts, a significant difference ($p < 0.001$).

Rank 1 males readily approached and pursued subordinates, but rarely bit them. Head bobbing, however, was frequently performed by dominant males, and comprised 21% of their aggressive behaviors. In all instances, it followed a chase and was very irregular in pattern and frequency. Second rank males exhibited head bobbing significantly less often ($p < 0.001$).

During sexual encounters, rank 1 and 2 males approached and pursued females readily. Rank 3 males seldom approached females, although individual behavior was variable and one would occasionally pursue a female that was usually avoided.

The readiness with which rank 2 males chased females strongly contrasts with their behavior toward rank 3 males. Of 39 instances of pursuit recorded for rank 2 males, only five were directed toward subordinates, implying the capacity for sex discrimination.

Although rank 1 and rank 2 males readily pursued females, rank 1 males were responsible for 62% of all sexual acts (Table V), whereas the contribution of rank 2 males (31%) was

significantly less ($p < 0.001$).

Rank 1 males, unlike subordinates, sometimes caught females, grasping the latters' tails in their jaws. Usually, the female escaped, and only one successful mating was observed. After a female escaped, dominant males, with head raised, occasionally searched the area of contact. Femoral rubbing was frequently performed by dominants during searches, whereas only three of 29 such instances observed were performed by rank 2 and subordinate males, a significant difference ($p < 0.01$). Femoral rubbing was not restricted to interactions with females, but often occurred following pursuit of subordinate males.

Thermoregulatory behavior was performed by all ranks and females (Table V). Basking was observed equally for all groups, usually shortly after emergence at the onset of the daily activity cycle. Burrow entering, a cooling behavior was performed most frequently by rank 1 males.

Dominant males feed more frequently than lower ranking males and females, but this difference was not significant, and there was no evidence of food competition. In one instance, a dominant male pursued a feeding subordinate, but the latter retained the prey, grasped in its jaws, and resumed feeding after the encounter. Because the food supply was mobile, and dispersed, foraging was not restricted to limited areas, and food sources were not dominated by high ranking males.

One group was observed for 4 weeks beyond the breeding season. Although a hierarchy was not detectable, males exhibited individualized behavior patterns. Male M146 was involved in fewer interactions than other males, and invariably fled upon encountering another male. However, it always approached and followed females, often chasing and biting them. In contrast, male M153 occassionally chased other males. It often followed, but never chased females, and occasionally exhibited femoral rubbing after such encounters, unlike male M146 which never performed this act. A third male exhibited neutral behavior, occasionally fleeing males, but never chasing either sex. No male showed both aggressive dominance and sexual activity, as observed for dominant males during the breeding season. The only male which showed no aggressive behavior was the one which readily chased and grasped females.

The Relation of Hierarchy Formation to Annual Physiological Cycles

Males exhibit aggressive behavior and establish hierarchies in late May, as the breeding season commences. The reproductive period continues through June and July, culminating by early August. From the time of emergence from winter dormancy, to late summer aestivation in August, the testes, abdominal fat bodies, and adrenals undergo seasonal changes in size (Table VI).

Following emergence in March, fat body deposition, in milligrams/gram body weight, is relatively low. During April,

Table VI. The Seasonal Cycle of Fat Body Deposition and Testicular and Adrenal Size Change. Data is expressed as means and standard deviations for each month.

Ratio	Month					
	March	April	May	June	July	August
Fat body wt./ Body wt. (mg/g)	22.5±17.2	47.6±22.1	27.6±51.2	9.2±24.9	25.2±42.9	152.5±170.6
N	6	11	18	23	24	17
Testes wt./ Body wt. (mg/g)	4.9±3.1	10.4±4.4	9.4±1.6	12.6±3.9	11.0±2.1	2.6±1.8
N	3	14	12	24	27	17
Adrenal vol./ Body wt. (mm^3/g)	.091±.034	.054±.025	.044±.025	.120±.059	.078±.034	.053±.015
N	3	12	12	26	9	7

Results are compiled from 1972-1974 data.

fat bodies double in size, due to increased foraging. By May, however, deposition has again declined as the breeding season approaches. During June, at the peak of the mating season, fat bodies atrophy, due to energy demands rising from increased activity associated with aggression and sexual activity. Depletion continues until late July, when aggression wanes and activity is again directed toward feeding and maintenance, causing increased deposition prior to the onset of aestivation in late August.

The annual testicular cycle was determined from the seasonal change in testes to body weight ratio (Table VI). Following emergence in March, testes are relatively small. Within a month, males exhibit marked testicular hypertrophy, although individual variation exists. Less variation is noted for June, when intraspecific aggression is most intense and hierarchies are established among captives. Hypertrophy continues until the end of July, when the decline in aggressive behavior closely corresponds to marked testicular atrophy. Relative testes size is minimal in August, when aggression is no longer observed.

Racerunner adrenals undergo a seasonal cycle of size changes related to activity. Males examined following spring emergence exhibit relatively large adrenal volumes (Table VI). Considerable individual variation occurs due to the many factors affecting adrenal activity including food availability, predation and climatic stress. In April and May, adrenal

atrophy indicates a decline in activity. Drastic hypertrophy is observed in June, coincidental with the formation of dominance hierarchies among captives. Increased activity coincides with testicular hypertrophy and fat body depletion.

A decline in adrenal volume commences in late July as intraspecific aggression diminishes, and captive males, which no longer form dominance hierarchies, exhibit marked adrenal atrophy.

Anatomical Indices of Social Rank

Dominant males were significantly heavier than second rank males ($p < 0.02$) and rank 3 males ($p < 0.001$). A similar relation was observed for body length (Table VII). In only five of 35 groups studied was the rank 1 male smaller than a subordinate. Since lizards were not grouped according to size, males of similar weight were occasionally placed together. In such instances, the factors which determined dominance were not apparent.

The relation of physiological state to rank was determined using various anatomical indices. Because observations indicated that dominant males were more active, the effects of rank on nutritive state were examined.

A comparison of mean stomach content to body weight ratios showed no significant difference between ranks, due to large individual variation (Table VIII). Thus, there was no indication of food deprivation among subordinates. Table VIII also shows that rank is not related to liver weight to body

Table VII. The Relation of Social Rank to Body Size. Body weight and snout-vent length expressed as means and standard deviations for each rank.

Rank	N	Body wt(g)	N	Snout-vent length (mm)
1	37	6.51 ± 1.68	37	64.5 ± 5.4
2	35	5.47 ± 1.71	35	60.9 ± 5.7
3	48	4.79 ± 1.44	48	57.9 ± 4.9

Results based on combined 1972-1974 data.

Table VIII. The Relation of Social Rank to Stomach Content and Liver Size.

Rank	N	Stomach content st/body wt(mg/g)	N	Liver wt/ body wt(mg/g)
1	22	28.2 ± 8.6	23	24.5 ± 5.2
2	23	26.2 ± 11.1	24	25.1 ± 5.3
3	27	27.5 ± 5.8	17	23.9 ± 5.3
Controls	20	29.6 ± 9.3	24	25.1 ± 5.3

Results combine 1972-1974 data.

weight ratios, a measure of energy storage and utilization.

Because the fat body cycle is seasonal, only males that had been maintained in captivity simultaneously were compared. No relation of rank to mean fat to body ratio is shown (Table IX). Rather, large individual variation was observed. Non-captive controls exhibit ratios similar to those of captives until August, when deposition by controls increases because they avoid contact and feed more. Apparently, captives do not keep pace because of limited food accessability and feeding inhibition due to lack of isolation.

Because reproductive behavior was only exhibited by high ranking males, the relation of dominance to reproductive potential was analyzed. For males removed from arenas in late June, there is no relation of relative testes size to rank (Table IX). The ratios of captives are similar to those of seasonal controls. Rank 3 males examined in mid-July, however, exhibit relatively smaller testes to body weight ratios. In late July, at the end of the breeding season, all ratios show testicular atrophy. In instances where a dominant male was smaller than a subordinate, the former usually possessed heavier testes.

Seminiferous tubules undergo a seasonal cycle of hypertrophy corresponding to testicular hypertrophy. Unlike testes size, however, tubule diameters are less dependent on body weight, and therefore serve as a more accurate index of testicular activity. Mean seminiferous tubule diameters of rank

Table IX. The Relation of Social Rank to Fat Body and Testes Weights, and Seminiferous Tubule Diameter. Means and standard deviations are listed. Control values were obtained from males not kept in captivity.

Variable	Social rank	Date of Removal from Arena: N	6-20 to 6-30	N	7-10 to 7-20	N	7-25 to 8-05
Fat wt./ body wt. (mg/g)	1	8	8.6±6.1	8	24.7±8.9	5	11.3±8.4
	2	7	10.9±5.5	7	14.7±10.3	5	15.6±19.7
	3	6	8.2±8.7	6	28.5±23.9	5	3.8±8.6
	Control	34	3.9±9.8	13	38.2±46.2	17	152.6±170.7
Testes wt./ body wt. (mg/g)	1	16	10.7±4.8	15	7.4±4.8	11	2.8±2.3
	2	15	10.6±3.4	13	9.5±7.3	10	3.3±1.7
	3	17	10.7±3.5	14	5.2±3.8	18	2.7±2.0
	Control	34	11.7±2.2	13	7.2±3.6	17	2.6±1.7
Seminiferous tubule diameter (mm)	1	14	0.186±0.047	14	0.174±0.040	10	0.112±0.027
	2	15	0.185±0.033	7	0.162±0.018	8	0.111±0.029
	3	15	0.177±0.032	10	0.137±0.030	12	0.106±0.019
	Control	29	0.185±0.024	13	0.162±0.049	12	0.097±0.024

Results based on combined 1972-1974 data.

3 males are smaller than those of rank 1 males (Table IX). This contrast is greatest in mid-July, when the difference is significant ($p < 0.05$), indicating a lower reproductive potential among subordinates. Throughout the breeding season, tubule diameters of captives are similar to those of non-captive controls.

To elaborate the relation of rank to reproductive state, the number of males per group that possess mature sperm in the seminiferous tubules and epididymus were compared (Table X). 62% of rank 1 males possessed sperm in the tubules in contrast to 50% of rank 3 males, although this test was not significant. The value for rank 3 males was likewise lower than the percentage obtained for seasonal controls (Table X). Surprisingly, rank 2 males exhibited a higher percentage of fertility than did dominant males, although the difference was not significant.

The presence of sperm in the epididymus was also less likely for rank 3 males as compared to rank 1 ($p < 0.05$). Again, rank 2 males exhibited a greater frequency of sperm presence.

Relation of Social Rank to Stress

Table XI lists variables selected as indicators of stress. The mean body weight change of captives is similar for rank 1 and rank 3 males. In contrast, rank 2 males show significant weight gain ($p < 0.001$). There was no observable seasonal trend for weight change, which was not related to

Table X. The relation of Social Rank to Fertility. Groups are compared for the presence of sperm in the seminiferous tubules of the testes, and the epididymus. Season control males, not kept in captivity, are also compared. The % of the males per group that possessed sperm is listed.

Group	Presence of sperm in testes		Presence of sperm in epididymus	
	N	% with sperm	N	% with sperm
Rank 1	35	62.8	18	66.6
Rank 2	30	66.7	16	75.0
Rank 3	38	50.0	21	35.7
Controls	48	65.6	53	63.7

Results based on combined 1972-1974 data.

Table XI. The Relation of Social Rank to Stress. Mean weight change during captivity, occurrence of precapture tail autotomy, and ratios of adrenal size in proportion to body weight are listed for ranks, and captive control males kept in isolation.

Rank	N	% body wt. change	N	Adrenal vol/ body wt (mm^3/g)	N	% occurrence of tail autotomy
1	46	-5.4 ± 7.6	20	$.070 \pm .021$	41	43.9
2	32	$+3.2 \pm 4.9$	17	$.081 \pm .035$	36	16.7
3	47	-4.7 ± 4.9	15	$.089 \pm .033$	48	27.1
Control	--	----	20	$.067 \pm .030$	--	----

Results combine data collected from 1972-1974.

the seasonal cycle of fat body deposition. Instead, individual weight change was highly variable.

The ratio of adrenal volume to body weight did not show a seasonal trend for captives, as observed for control males (Table VI). Apparently, the arena environment modified the effects of the seasonal cycle, so that differences in relative adrenal size were instead related to rank. Rank 3 males exhibited significantly larger adrenal volumes than rank 1 males ($p < 0.05$), indicating greater stress (Table XI). Captive control males, isolated in arenas similar to those holding hierarchy males, exhibited the lowest mean adrenal ratios. Thus, it appears that grouped males undergo more stress than isolated ones, and that among the former, subordinates are subjected to maximum stress.

The occurrence of tail autotomy results in regeneration, with a marked alteration of scale patterns, rendering it possible to determine whether a lizard had undergone autotomy at some period of its life history. Dominant males exhibited the greatest frequency of autotomy (Table XI). The percentage occurrence of pre-capture autotomy was highest for rank 1 males, significantly lower for rank 2 males ($p < 0.01$), and intermediate for rank 3 males, indicating that rank 1 males are subjected to a greater overall degree of predation than subordinates.

Discussion

The observed linearity of six-lined racerunner hierarchies was also reported by Hardy (1962). Carpenter (1960), however, noted that the rank of intermediate males was difficult to determine and hierarchies were nonlinear. In the present study, the small number of animals per group likely allowed greater individual recognition, thus permitting a more consistent pattern of response, i.e., animal A would readily recognize animal B.

As in this study, male dominance characterized the peck orders observed by the above investigators. However, larger females occasionally ranked higher than small males (Carpenter, 1960). This may result from the inability of small males to discriminate between sexes in a large group. The fact that dominance shifts usually occur when a new lizard is introduced (Hardy, 1962), momentarily confusing individual recognition, supports this idea. In the present study, utilizing small groups, low ranking males seldom fled females except at the end of the breeding season.

Hierarchies were maintained by frequent aggressive interactions. Dominant males were aggressive throughout the confinement period. In contrast, Hardy (1962) observed that most interactions involve approach-avoidance encounters, with little actual pursuit or aggression. However, Carpenter (1960)

observed frequent aggressive interactions involving pursuit and biting, both for captive groups and field observations.

The interactions which characterize dominance hierarchies are similar to those observed in the wild, with no evidence of territorialism. Thus the relationships of dominant to subordinate animals, and any advantages associated with dominance, are of ecological significance.

Dominant lizards emerge at the onset of the daily activity cycle after subordinates. Early emergence may allow the latter added forage opportunities, minimizing encounters with dominant males. Following emergence, the duration of a lizard's activity period was not related to rank. In contrast, Carpenter (1960) found that dominants usually emerged first and remained active over longer periods. Perhaps the large groups he studied suffered greater feeding competition, forcing dominants to spend more time in activity.

Dominant males, regardless of the duration of emergence, were more active than subordinates and participated in most of the interactions observed, in agreement with Carpenter (1960). This has also been shown for a number of mammalian species (Adams & Finn, 1972; Lloyd & Christian, 1967).

Previous studies indicate that body size and rank do not always correspond (Carpenter, 1960; Hardy, 1962). However, both utilized snout-vent length as the body size indicator. In the present study, considerable body weight variation occurred among males of similar length, and weight differences

between ranks were more pronounced than length differences.

Racerunner lizards exhibit color dimorphism which apparently serves in agonistic displays between males (Noble & Bradley, 1933). Observations from the present study support this. However, there was no indication that rank was related to color intensity, which was extremely variable among males, in agreement with the observations of Hardy (1962). Thus, aggressive dominance is expressed by behavior and postural displays rather than by morphological cues.

One such threat behavior is head bobbing, performed by dominant males following aggressive interactions. Head bobbing has also been reported by Hardy (1962) but was not included in the repetoire described by Carpenter (1960). Since it invariably followed aggressive interactions, it is considered a threat behavior but the act may be vestigal since it is only occasional in occurrence.

The seasonal onset of aggression in six-lined racerunners is controlled by the testicular cycle, as for many vertebrates (Van Tienhoven, 1969; Guhl, 1961). Aggressive interactions occur only during the breeding season and, in wild populations, serve to maintain spacing, thus lessening mate competition. The disappearance of aggressive behavior corresponds to the termination of the reproductive period, resulting in mutual avoidance.

Anatomical indices of reproductive state confirmed behavior observations. Because relative testes size, commonly

used as a reproductive index, is dependent on body size, other indices proved more useful. Seminiferous tubule diameter, influenced by testicular activity rather than body size, and the presence or absence of sperm in the testes and epididymus are better indices.

These indices showed that the reproductive state of racerunner lizards was related to rank, confirming behavior observations. Although rank 1 males exhibit the highest frequency of sexual behaviors, rank 2 males are sexually active as well. Anatomical indices show similar findings, in agreement with other studies which show that the dominant male of a vertebrate hierarchy is not necessarily the most sexually fit (Wood-Gush, 1957). In nature, the most aggressive male might mate less often than a male of intermediate rank which expends less energy in aggressive confrontations. The lowest ranking males are less sexually active and less fertile. A few rank 3 males were subadult; most, however exhibited testicular hypertrophy and adult sexual coloration. Subordinates may have suffered reproductive inhibition due to stress from interactions with dominant males, as observed in other vertebrate species (Christian, 1963; Flickinger, 1961; Guhl, 1961). Whereas the present study does not show that subordinates suffered reproductive inhibition as a result of aggression by dominant males, the activity and behavior was certainly inhibited by the latter.

Following encounters with females, dominant males

perform femoral rubbing. This has also been reported by Carpenter (1962), and occurs in other species as well (Cole, 1966). Its significance, and the function of the femoral glands, have not been determined. During copulation, males rub their femoral pores against the females' body. This may serve as a tactile stimulus, activating ovarian responses or facilitating sperm transport and fertilization. Since males also exhibit this behavior following aggressive encounters, the glands may secrete pheromones, attracting females or repelling males (Cole, 1966). Females also possess femoral pores, which do not hypertrophy during the breeding season, as do males'. Observation suggests a possible role in mate attraction via olfaction. Males often maintain a vigil near a female's burrow, and perform behaviors indicating nonvisual awareness of the occupant's sex (Carpenter, 1962). An investigation of behavioral responses to femoral gland exudates is planned.

Mating behavior, including femoral rubbing, is occasionally observed following the termination of the breeding season, when anatomical indices denote testicular quiescence. At this time, aggressive behaviors are not observed, indicating that aggressive and mating behaviors operate in distinct hormonal milieus, i.e., neurohormone interactions necessary for eliciting sexual behaviors persist beyond the extinction of aggressive responses.

When food is limited, the nutritive state and feeding

behavior of racerunner lizards is markedly affected by social status. Dominant males grew more rapidly and fed more readily than did subordinates when studied in enclosures where food is placed in a limited area of the arena, allowing for severe feeding competition (Hardy, 1962). In the present study, arenas contained adequate vegetative cover, food was randomly distributed, and foraging encouraged. The readiness with which subordinates foraged indicates an absence of food competition or starvation-induced stress. Anatomical indices likewise confirmed that nutritive state was not related to status. Relative stomach content weights did not differ between ranks. Relative liver size, which indicates glycogen content and is affected by seasonal fluctuations in diet (Telford, 1970) was not related to rank. Fat body weight, which, in lizards, is influenced by food availability (Licht and Gorbman, 1970), is likewise not related to social rank.

While rank 1 and 3 males underwent a similar average weight loss, rank 2 males exhibited a significant weight gain. This appears to contradict the conclusions drawn of the basis of fat body, liver and stomach content comparisons, and cannot be accounted for at present.

The seasonal cycle of adrenal size observed for racerunner lizards is similar to that described for other reptilian species (Gabe, 1970). Since gland size reflects adrenal activity (Lofts et al., 1971; Wilhoft, 1964), six-lined racerunner lizards apparently exhibit maximal adrenal activity

during the breeding season, due to increased aggression and reproductive activity. In the present study, relative adrenal size is maximal for subordinate males. This relation has been established in studies of dominance relationships of a number of vertebrate species. Bronson (1964) and other investigators (Brain, 1972; Terman, 1969; Christian and Davis, 1964) have shown this for mammalian species, and Siegel (1959) and Flickinger, (1961) correlated adrenal size to status in avian hierarchies. Archer (1970) has shown, for mice, that adrenal hypertrophy in subordinates is a result of aggressive interactions. Fewer such studies have been performed for heterothermic species, although Erickson (1967) related low rank to adrenal hypertrophy in sunfish hierarchies. The present study offers the first indication of such a relationship for a reptilian species. Since subordinate animals did not exhibit food or thermal stress, hypertrophy likely resulted from aggression-induced stress.

Tail autotomy occurs in many lizard species and is assumed to result from encounters with predators. Autotomy also results from intraspecific aggressive interactions, however. Carpenter (1960) has described incidents in which a male, grasping another's tail, induced it to autotomize. In the present study, no such instances were observed. However, males were occasionally found in live-traps with freshly autotomized tails. In such instances, a second male was also present, indicating that autotomy resulted from an aggressive

interaction.

The frequency of occurrence of precapture autotomy was highest in rank 1 males. Fitch (1958) found that frequency of occurrence was positively correlated with size, and Schall (1974) noted that males of a related species, Cnemidophorus arubensis, undergo autotomy much more frequently than females. Males are more susceptible than females, and large (high ranking) males more than subordinates possibly because the high activity level of dominant males more frequently exposes them to predators and conspecifics. Based on trap records, male racerunners, in contrast to females, more readily forage in open areas where risk of exposure to avian predators is greater.

The separation of members of a captive dominance hierarchy by rank categories is useful in determining the relationship of aggressive dominance to behavior and physiological state. Dominant males are readily distinguishable on the basis of size alone, but dominance is also associated with high levels of activity and aggression. Subordinate males, in contrast, exhibit adrenal hypertrophy, possibly indicating relatively greater stress as a result of aggression by dominants. This stress may contribute to their relative inactivity and may inhibit sexual behavior. There is no indication that stress in subordinates is related to differences in food accessability or nutritive state.

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