DOMINANCE RELATIONS BETWEEN BENNETT'S WALLABIES, *Wallabia rufogrisea frutica*, CONFINED TO A YARD

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ABSTRACT

DOMINANCE RELATIONS BETWEEN BENNETT'S WALLABIES, *Wallabia rufogrisea frutica*, CONFINED TO A YARD

By

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This was a three part study consisting of (1) an analysis of dominance; (2) the establishment of baseline dominance relationships between individuals; and (3) a manipulation: the periodic removal of the dominant male. The *Ss* were seven Bennett's wallabies: two mature males, one two-thirds grown male, and four females.

In the first part, the dominance patterns of male-male, male-female, and female-female compositions were analyzed. During these observations particular acts, termed identifiers, were selected as defining the occurrence of aggression and avoidance, which were the essential components of dominance. Male-male dominance was scored when one male avoided any direct approach by another; but for male-female and female-female dominance a fight, a blow, or a growl plus a chase was required. Fighting dominance and unopposed dominance were distinguished.

In the second part, a baseline of dominance was established between each individual and every other, but with particular emphasis on the male-male composition. In the male-female and female-female compositions fighting dominance and unopposed dominance were not tallied separately due to the occurrence of many marginal instances and to the smaller number of total dominations. The results were, that dominance relations were consistent in all three sexual compositions, but were very frequent in the male-male composition, moderately frequent in the male-female composition, and rather infrequent in the female-female composition.

In the third part, the effects on these baselines of the absence of the currently dominant mature male, and of his subsequent returns, were measured. There were two such removals for periods of 18 days each, and one removal for only 48 hours. The results were, that when a mature male was dominant over another he stayed so until removed: but on both of the returns after an 18 day absence complete reversals occurred (after agitated adjustment during the return days). However, when the dominant male was returned after only a 48 hour absence an exceptionally violent fight ensued, with the original dominant male winning a complete victory and continuing his dominance as before. One mature male always dominated the immature male, but dominance between the other mature male and the immature male varied with conditions.

The highest degree of male-male dominance was expressed by a maximum of unopposed dominance and a minimum of fighting dominance, because in such case the subordinate fled on the dominant's approach instead of remaining to fight. Dominance was most extreme just after a dominance reversal; fighting increased with time. The most even balance of unopposed and fighting dominance between the mature males was in the base-line period, when one had presumably been dominant for over a year.

Both mature males always dominated all females. The immature male dominated two females; the other two dominated him.

One female overwhelmingly dominated the other females in the first three periods but by the last period she had lost dominance completely; some females had few or no female-female dominance relationships.

Most of male-female and female-female aggression and dominance arose from what appeared to be frustrated sexuality which occurred after a period of physical contact, whereas male-male dominance was frequently expressed without preliminary physical contact between the males, and often without the subordinate being in contact with, or even in the proximity of, a female.

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INTRODUCTION

First studies of a little known species, as is Bennett's wallaby, may well be done under semi-natural conditions. This usually means, in a large outdoor enclosure. Fighting and dominance then occur more spontaneously than when they are induced by laboratory manipulations, and they can be more accurately analyzed than when they are studied in the wild.

The Dearth of Behavioral Information

There is but one report which is partly concerned with wallaby behavior. Immelman (1965) stated that Wallabia agilis live in pairs on well defined home ranges, but that defense of these is uncommon. Otherwise, although a few Macropodids (kangaroo-type marsupials) have been studied, only Stodart (1966) seriously considered dominance. She confined the boodie, Bettongia lesueuri, to a 3/8 acre enclosure and described dominance patterns, including a count of 95 "aggressive chases". She found that "The males were aggressive towards one another and towards one female in the other's social group. One was dominant over the other. Some evidence was obtained suggesting a hierarchy among the females." Sharman and Calaby (1964) described male fighting, but not

dominance, in captive red kangaroos, Megaleia rufa; Kirkpatrick (1966) did not mention dominance in wild grey kangaroos, Macropus canguru, though he said "Rivalry between males over a female in oestrus occurred, but was observed infrequently." He also stated that young males are separated from their mothers by older males who consider them rivals. The Breedens' extended observations of a group of grey kangaroos (1967) found one male to be the invariable winner of the post dawn fights and noted mild conflict between females. No detailed behavior analyses were made. Caughley (1964) found no "hierarchy of dominance" in wild red or grey kangaroos.

The Advantages of Semi-natural Observation

Dominance studies under laboratory, wild, and semi-wild conditions have characteristic virtues and defects, and discrepant results can occur from the use of different measures of dominance under different conditions (Scott, 1966).

Wild conditions present all the natural variables in natural interaction. Individual variables such as species, age, size, sex, sexual condition, type and degree of acquaintanceship, and number of animals observed; and environmental variables such as territorial, spatial, water, or other requirements for sleeping, mating, raising young, or food-seeking, are all present: and are often uncontrolled

if not unnoticed. Also, observations are likely to be irregular and imprecise.

The laboratory permits close observation and precise control of a few variables, by distorting natural variables and introducing artificial ones. Examples are the use of domestic strains, cramped indoor quarters, and especially the artificial induction of fighting: by footshock, by food competition, by operant and classical conditioning, by extinction, by pairing in a very crowded arena, and even, in mice, by dangling one animal by the tail against another. Such approaches may require counting one relevant response and ignoring others, or even measuring only the duration of attack and ignoring its components (Azrin, Hutchinson, and Hake, 1966). The pertinence of such results to dominance in nature (which includes linear, triangular, monarchial and oligarchical hierarchies: Marler and Hamilton, 1967) remains to be demonstrated.

The semi-natural method is a good compromise. Close observations can be made on animals enjoying reasonable freedom, which provides otherwise unobtainable information. Such information was sought in a three part study.

The goal of the first (analytical) part was to analyze dominance patterns in great detail, and to identify their occurrence explicitly and exclusively by the occurrence of particular behaviors in the various compositions. Thus future investigators can agree or disagree exactly as to what

constitutes aggression and avoidance, which are the two requisites for the occurrence of a domination. While some studies display precise analysis of the kind aimed at here (Wiepkema, 1961; Allen and Banks, 1968); others rely upon "observer agreement" or even upon some unstated ground to resolve all problems of behavior classification.

The goal of the second (baseline measurement) part was to establish the frequency and degree of the dominance relationships between individuals, and the goal of the third (manipulative) part was to observe the effect on these relationships of removing the dominant male for a time and then replacing him. Such a removal involves many possible variables which clearly affect results. For example, do the combatants meet in one's home area, or on neutral ground? Do they forget one another or their surroundings after separation? If so, how long does forgetting take? Does isolation stimulate or depress aggressive behavior? These questions have been only somewhat explored even in such common species as chickens (Guhl, 1953; 1958; 1961) and mice (Ginsburg and Allee, 1942; Scott, 1966). Nevertheless it seemed well to make a beginning with wallabies, and to see whether altering a psychological (non-physiological) variable could alter dominance relations.

METHOD

This study was begun in January, 1968, and was completed in September, 1968. All items except procedure and results were identical in all three parts of the study. The procedure used in each part is specified at its beginning. The baseline and manipulative parts generated both quantified and qualitative results. Each of the quantified results sections follows its own procedure section and gives the frequencies of the various kinds of dominations. The qualitative results, which are a summarized verbal description of important dominance and dominance-related behaviors, are distilled from all three parts. These results appear just prior to the discussion.

Subjects

Ss were two grown males of nearly equal size (RK and Cal); one two-thirds grown male (Flo); three grown females (Ari, Las, and Con); and one nearly grown but sexually mature female, Del. Del and Flo were born in the enclosure. Del was first observed in Ari's pouch in early April, 1967; Flo was first seen in Con's pouch in May, 1967. The others have been quartered at Michigan State over a year; they were

obtained from the State Animals and Birds Protection Board of Tasmania. All are accustomed to the investigator and other humans in their yard; they most often ignore familiar humans unless closely approached.

Living Area

This was an outdoor enclosure 58.5 ft. x 109 ft., with access to a heatable indoor stall.

Diet

Grass growing in the yard was the staple, except in winter. Lettuce and rolled oats, an iodine salt block, tea added to water, plain water, a daily vitamin spread sandwich, and wood chips (refuse from guinea pig cages) were always available. Pieces of wood were often eaten when obtainable.

Apparatus

A portable tape recorder for note taking, a stool on a platform for observation, and 7 x 35 binoculars for seeing details, were used. To obtain the line drawings used in Figures 4-8, a 16 mm movie camera was used to film dominance sequences. Then a tracing table which reflected any selected frame from a mirror angled at 45 degrees onto a horizontal glass surface was used to trace the drawings.

PART I: ANALYSIS

Purpose

The purpose was to determine precisely which behaviors signified dominance and subordination, and in which contexts.

Procedure

Operational definitions of aggression and avoidance were sought, to distinguish the various elements of dominance and subordination from each other and from non-dominance social behaviors. One hour observations were made almost daily for several months, using each of the 24 hours to see when aggression occurred.

Results

General dominance (defined below) occurred at all hours, but it peaked during maximum social activity, which is post-midnight, especially from 2-3 A.M.[1] Fighting, particularly vigorous male-male fights, occurred almost entirely from dawn until 2-3 hours later. This conforms with Breedens' (1967) finding for the grey kangaroo in the wild.

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[1]J. I. Johnson, Unpublished data in Progress Report, Research Grant No. NB 05982: Development of Afferent Nervous Centers.

Some aggression-avoidance patterns stood out clearly from the matrix of social behavior but others were only marginally certain and required special effort both in the individual recognition of, and in the categorization of, behaviors. The latter required the definitions of terms set forth below. Problems in recognition of marginal behaviors are discussed in Appendix 1.

Definitions of Terms

Ss paired according to gender (male-male, male-female, and female-female) were termed compositions. Compositions generated classes, which were those social behavior groupings in which physical contact usually occurred. These classes were (1) dominance, (2) grooming, (3) sexuality, and (4) unclassified. Essentially non-contact behaviors such as grazing or resting were not considered, even when they occurred in mutual proximity (henceforth defined as one meter or less).

At any time, which class or sub-class occurred within a composition was determined by the appearance of an identifier, which comprised a component or components unique to that composition. The class of dominance required each animal to supply an identifier. One animal had to identify aggression, and the other, to identify avoidance, as these were the essential sub-classes of the class of dominance. Since the other classes of behavior were considered only insofar as

they related to dominance or were to be distinguished from it, sub-classes were not devised for them. Therefore they were identified by one animal even though the other remained passive. (In default of an identifier the unclassified class was invoked.) A component is an overt movement such as pawing or hopping. Since an identifier can by definition only occur in one class or sub-class, when one appears it automatically defines the class or subclass. See Appendix 2 for a further discussion of the goal of this analysis.

Though the male-male composition generated mostly dominance, the other compositions generated various other identifiers so defined as to create the four classes. These classes evolved to and from each other (as judged by the appearance of the various identifiers) and sometimes occurred simultaneously. This complexity requires a brief description of the non-dominance identifiers: the dominance identifiers are then defined in detail. Appendix 3 discusses the results of the dominance analysis in more detail.

Identifiers of Non-dominance Behaviors

Grooming

Either nibbling with the lips or licking another's body exclusive of the nose, pouch, and genital regions.

Male-female Sexuality

By males, serpentine tail movements, nosing the vagina or ground near it, penis eversion or erection when in female

proximity, and mounting: Pressing the body closely against the female from the rear while clasping the arms around her back just behind her shoulders; or a close attempt at mounting. By females, nosing the penis or scrotum. By male and female, copulation.

Female-female Sexuality

This is identified as in male-female sexuality, except for the absence of penis and scrotum involved behaviors.

Unclassified

Unclassified nosings and pawings occurred in male-female and in female-female interactions.

Identifiers of Dominance Behaviors

In all cases below, if the movement was adequately performed physical contact with the other S was not essential.

I. Aggression Identifiers

A. Unopposed aggression

1. Male-male unopposed aggression

a. step directly toward, or

b. hop directly toward, another S from any distance; or if in proximity,

c. nose jab: moving the nose and head directly at another S.

d. one-hand blow: a semi-circular punch, like a boxer throwing a hook.

e. two-hand blow: both hands thrust simultaneously at another S, claws extended.

f. kick: a leap into the air with both feet thrust at another S (one foot alone is never used).

2. Male-female and female-female unopposed aggression

a. growling by either S plus a pursuit

b. one-hand blow

c. two-hand blow

d. kick

e. non-avoidance subsequent to a blow or kick delivered by the other animal, as defined immediately above (I, A, 1; d, e, and f).

B. Fighting aggression

1. Male-male fighting: mutual pawing

2. Male-female and female-female fighting: mutual pawing plus either

a. both Ss rising up off the metatarsals to the tarsals alone and remaining so while pawing (concomitance is essential), or

b. a blow or a kick, as defined above (I, A, 1; d, e, and f)

c. non-avoidance subsequent to a blow or kick delivered by the other animal, as defined above (I, A, a; d, e, and f).

II. Avoidance Identifiers

A. Retreat: at least one step or hop anywhere in a semicircle away from the other S, but the retreater's head must not originally be faced directly away from the aggressor (except on the second or more of subsequent retreats during a series of aggressions, when it is permissible). A retreat was defined as only one retreat until forward motion stopped. If forward motion was

resumed while the pursuer either continued the old chase or, having stopped, began a new one, a second retreat was scored, and so on. Or,

B. Turn-away: Alighting after delivering a kick with the body facing at least 90 degrees away from the other's front.

A discussion of possible errors made in this analysis is found in Appendix 4. Appendix 1 discusses the problem of classifying marginal behaviors, which existed even if the classification scheme was correct.

PART II: BASELINE MEASUREMENT

Purpose

The purpose was to determine what if any measurable dominance relationships existed between the Ss.

Procedure

Dominance relationships between each S and every other S were examined in 16 observation periods over a span of 18 days. This constituted Period 1 (see Table 1). Observations began about 6:30 A.M., lasted one hour, and were made about six days per week. Male-male dominance got primary emphasis, but the other dominance compositions were also noted, and it is believed that few occurrences of dominance were overlooked. In male-male fighting, unopposed dominance and fighting dominance were tallied separately and were also totalled; in the other compositions only total dominance was scored. Efforts were made not to score marginal instances of dominance.

Results

Dominance totals are shown only for the completed Period 1. Daily totals are not shown but they varied greatly (from 0 to 27).

Male-male dominance (see Figures 1, 2, and 3, and Table 2).

TABLE 1

Summary of Durations of Periods in Days; of Males Present During Each Period; and of Hours Observed Each Period

Period	Span (Days)	Males Present	Total Observation--Hours
1	18	RK, Cal, Flo	16
2	18	Cal, Flo	16
3	25	RK, Cal, Flo	22 incl. return day*
4	18	RK Flo	16
5	25	RK, Cal, Flo	22 incl. return day*
6	2	Cal, Flo	1 plus later "spot checks"

*Cal and RK were returned in mid-afternoon. A return day observation was made for an hour immediately after each return.

FIGURES 1-3

Figures 1-3 show the dominations scores by each male against each other male. Fighting dominations, unopposed dominations, and the totals of both types are shown for the five main periods. All dominations which were observed and scored are shown, except for those occurring on return days.

Some of the histograms in periods 3 and 5 have an upper, speckled portion which is separated by a short horizontal line from the typical lower portion. These speckled portions show all scores made in days beyond the regular 16 days of observation, and reflect that there were actually 22 observation days in periods 3 and 5. The division facilitates comparison with periods 1, 2 and 4, which contained only 16 days of observation.

The scores for the 16 days in periods 3 and 5 are actually taken from days 2-17 inclusive, because in both cases day 1, the return day, contained erratic adjustment behavior which was atypical.

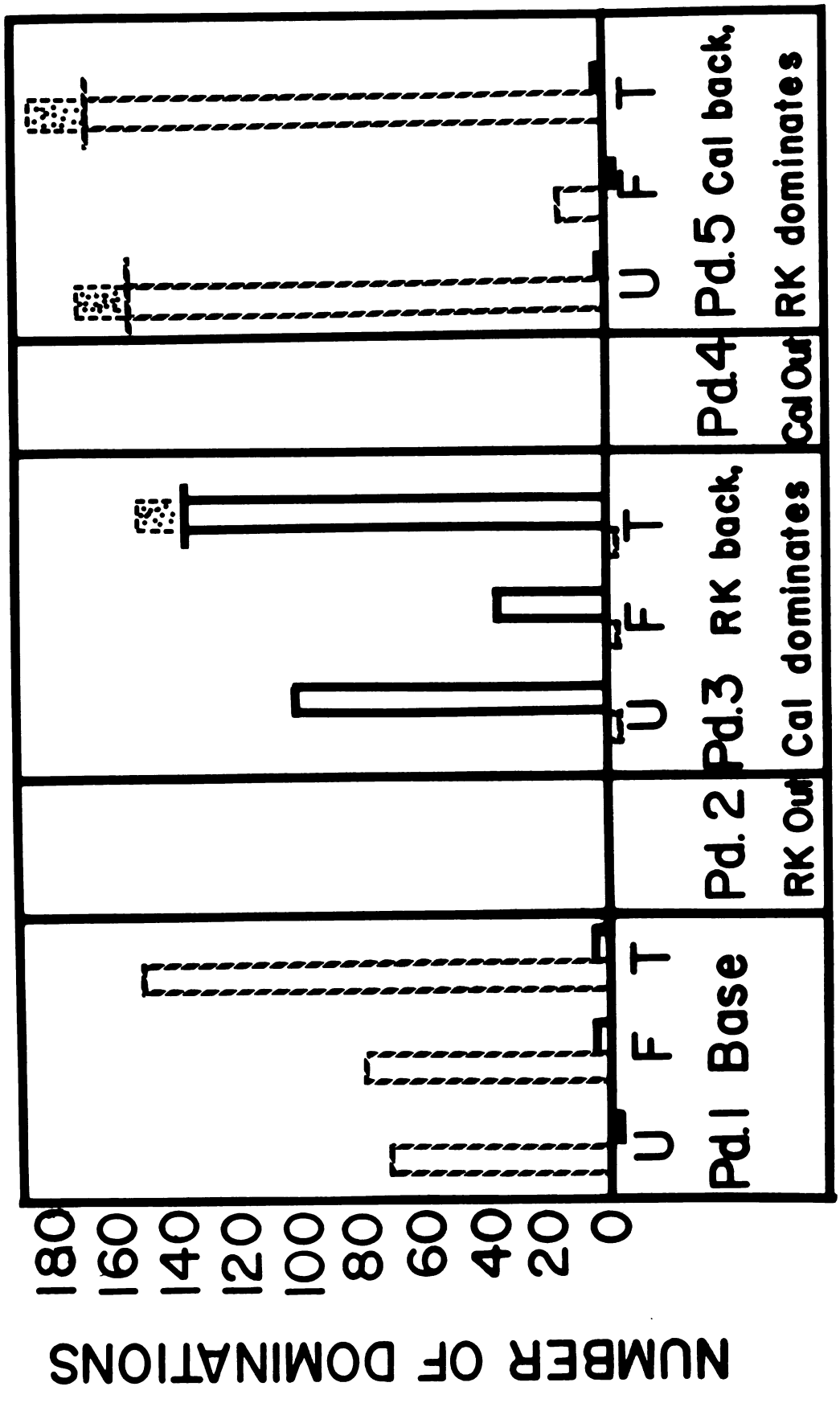

Figure 1. Dominance relationships between the two mature males, RK and Cal.

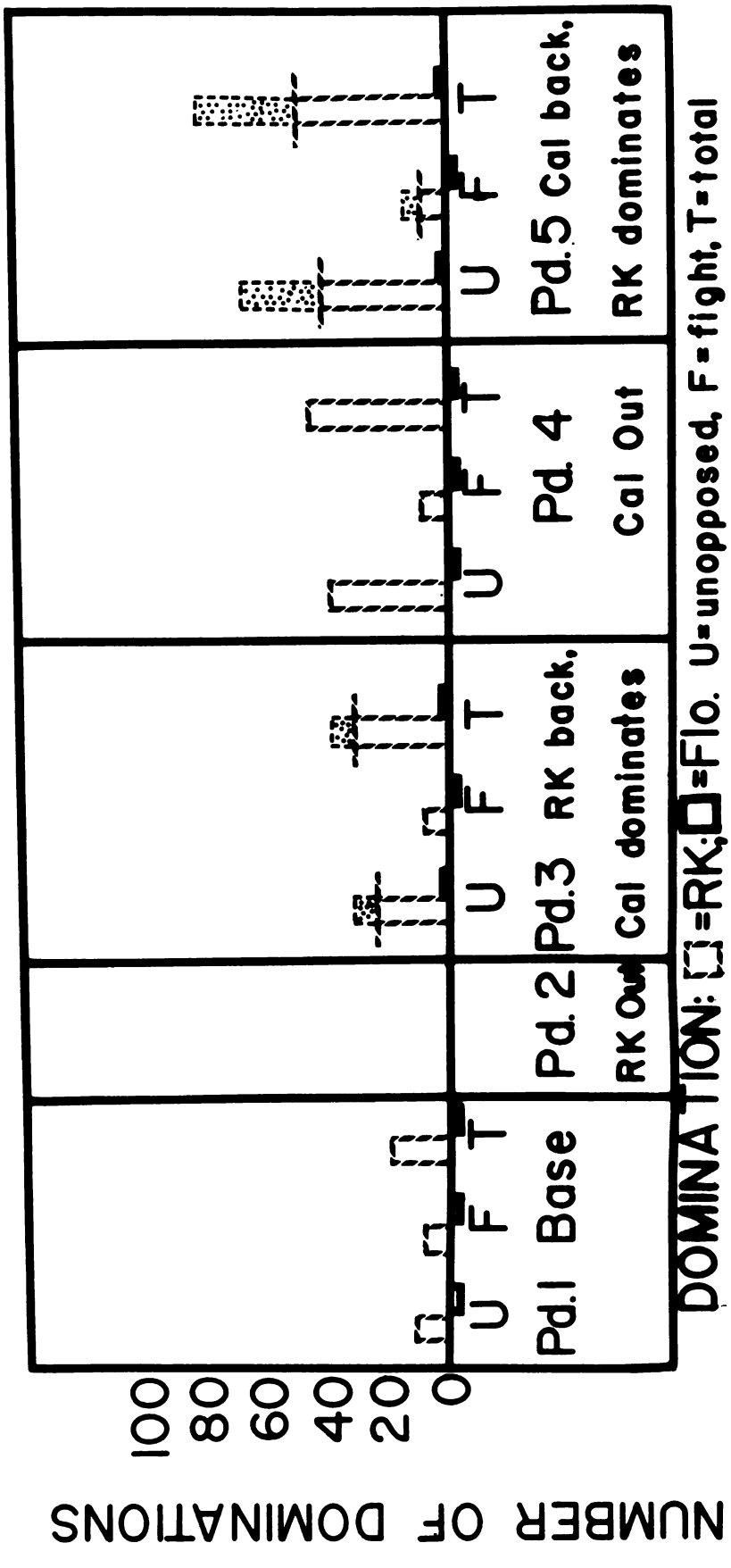

Figure 2. Dominance relationships between the mature male, RK, and the immature male, Flo.

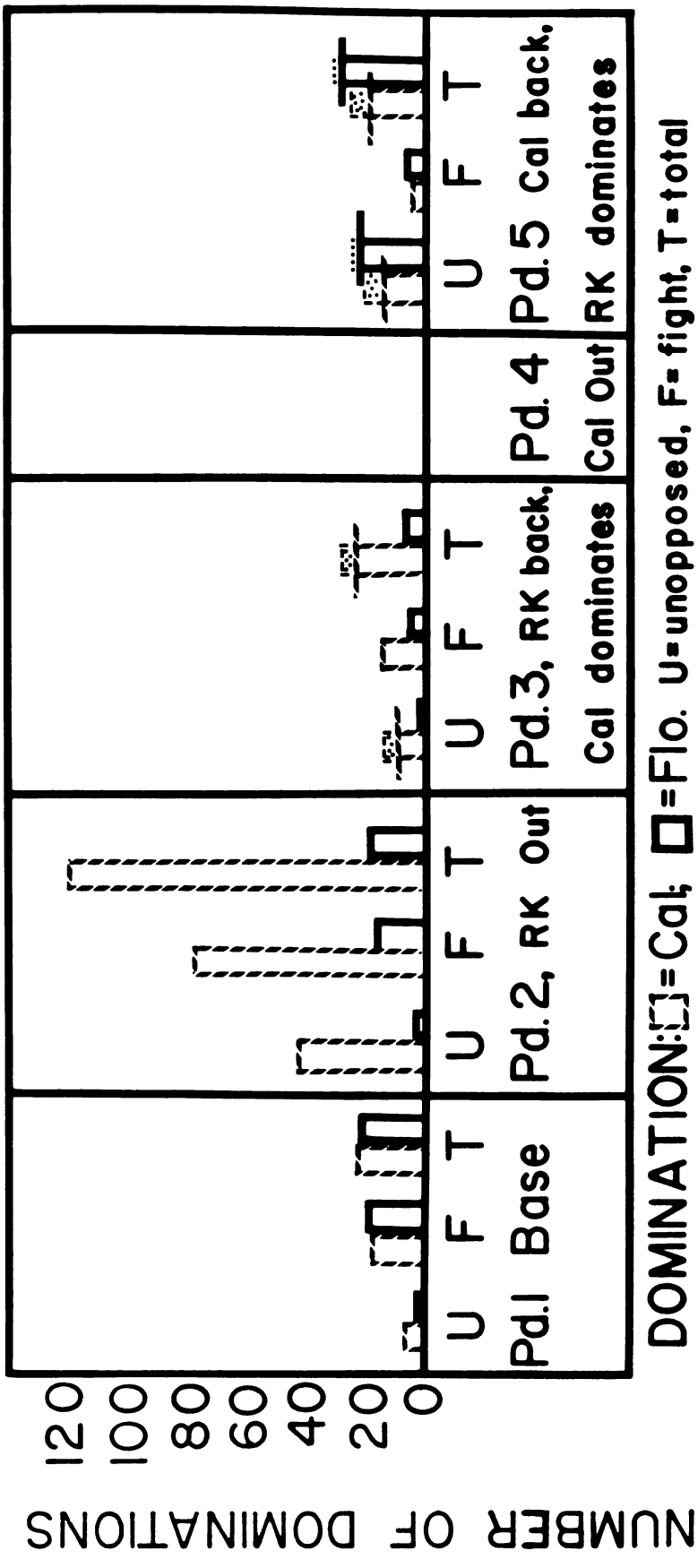

Figure 3. Cal-Flo dominance.

TABLE 2

Male-male Dominations

Periods of 16 Days			I						II			III
			RK	CAL	RK	FLO	CAL	FLO	RK	CAL	FLO	E
		U	71	0	11	0	5	2	82	5	2	89
	1	F	79	4	8	0	17	19	87	21	19	127
		T	150	4	19	0	22	21	169	26	21	216
		U					42	2				
	2	F					77	16				
		T					119	18				
		U	0	100	23	1	9	1	23	109	2	134
	3	F	0	35	7	0	14	5	7	49	5	61
		T	0	135	30	1	23	6	30	158	7	195
		U		*	38	0						
	4	F			7	0						
		T			45	0						
		U	152	1	41	1	14	22	193	15	23	231
	5	F	14	0	7	0	4	6	21	4	6	31
		T	166	1	48	1	18	28	214	19	29	262

*Only 11 days were observed and scored in Period 4

(U = unopposed, F = fighting, T = total) Section I contains the total dominations by each male considered as a member of each pair; Section II contains the total overall dominations by each male; Section III contains the total dominations by all males for the periods.

The results of the RK-Cal composition were:

1. RK dominated Cal completely.
2. RK's dominations over Cal were rather equally divided between unopposed dominations and fighting dominations.
3. RK's number of total dominations was large (150).
4. Of the few dominations scored by Cal over RK, all were fighting, none were unopposed.

The results of the RK-Flo dominance were:

1. RK dominated Flo completely.
2. RK's dominations were fairly equally divided between unopposed (11) and fighting (8).
3. The number of RK's total dominations over Flo (19) was only 1/8 the number of his dominations over Cal.
4. Flo scored no dominations over RK at all.

The results of the Cal-Flo dominance were:

1. Cal and Flo had nearly identical domination totals.
2. Cal and Flo's total dominations summed (43) were only a little over 1/3 the number of RK's dominations over Cal.
3. In unopposed dominations Cal outscored Flo 5 to 2.

Male-female dominance (see Tables 3 and 4, page 21, and Table 5, page 23).

TABLE 3

Total Dominations by Each Male Over All Females Combined; and by All Females Combined Over the Immature Male, Flo, and by Him Over Them, For All Periods

Period	CAL	RK	FLO	
			Dominations	Subordinations
1	14	14	14	19
2	29	0	5	11
3	30	5	3	8
* 4	0	15	8	2
5	27	21	13	4
Total	100	55	43 (85)	44

* Only 11 days were observed and scored in Period 4

TABLE 4

Total Dominations by Each Female Over All Males Combined and Over All Females Combined

Period	ARI		LAS		DEL		CON	
	Male	Female	Male	Female	Male	Female	Male	Female
1	13	7	5	1	1	0	0	0
2	9	23	0	1	1	0	1	0
3	6	14	2	0	0	0	0	1
* 4	2	6	0	0	0	0	0	0
5	4	3	0	0	0	7	0	0
Total	34	53	7	2	2	7	1	1
Total	87		9		9		2	

* Only 11 days were observed and scored in Period 4

1. The total number of male-female dominations was more than 3.5 times the number of the male-male dominations (61 to 216).
2. Both mature males dominated all females completely and equally (Cal, 14 to 0; RK, 14 to 0).
3. Flo dominated Con strongly and Del slightly (12 to 0 and 2 to 1); but was dominated strongly by Ari and somewhat by Las (13 to 0 and 5 to 0).

Female-female dominance (see Table 4, page 21, Table 5, page 23, and Table 6, page 24.

1. Total female-female dominations were only 1/27th the number of male-male dominations (8 to 216).
2. Ari was the dominant female. She scored 7 of the total of 8 dominations: 1 over Las, 2 over Del, and 4 over Con.

TABLE 5

Male-female and Female-female Dominations for All Periods

Period	Cal	Ari	Cal	Las	Cal	Del	Cal	Con	RK	Ari	RK	Las	RK	Del	RK	Con
1	4	0	6	0	2	0	2	0	6	0	1	0	6	0	1	0
2	7	0	17	0	2	0	3	0	---	---	---	---	---	---	---	---
3	8	0	13	0	1	0	8	0	0	0	0	0	4	0	1	0
* 4	---	---	---	---	---	---	---	---	6	0	1	0	6	0	2	0
5	11	0	0	0	11	0	5	0	5	0	0	0	16	0	0	0
Total	30	0	36	0	16	0	18	0	17	0	2	0	32	0	4	0

Period	Flo	Ari	Flo	Las	Flo	Del	Flo	Con	Ari	Las	Ari	Del	Ari	Con	Las	Del	Las	Con	Del	Con
1	0	13	0	5	2	1	12	0	1	0	2	0	4	0	0	0	1	0	0	0
2	0	9	0	0	0	1	5	1	2	0	11	0	10	0	0	0	1	0	0	0
3	0	6	0	2	1	0	2	0	2	0	10	0	2	0	0	0	0	0	0	1
* 4	0	2	0	0	4	0	4	0	0	0	4	0	2	0	0	0	0	0	0	0
5	1	4	0	0	10	0	3	0	0	0	0	7	3	0	0	0	0	0	0	0
Total	1	34	0	7	17	2	26	1	5	0	27	7	21	0	0	0	2	0	0	1

*Only 11 days were observed and scored in Period 4.

TABLE 6

Total Subordinations by Each Female to the Combined Mature Males, and to the Immature Male; and to the Combined Females for All Periods

Period	ARI			LAS			DEL			CON		
	Male	Female		Male	Female		Male	Female		Male	Female	
	RK-Cal	Flo		RK-Cal	Flo		RK-Cal	Flo		RK-Cal	Flo	Female
1	10	0	0	7	0	1	8	2	2	3	12	5
2	7	0	0	17	0	1	2	0	11	3	5	11
3	8	0	0	13	0	2	5	1	11	9	2	2
* 4	6	0	0	1	0	0	6	4	4	2	4	2
5	16	1	7	0	0	0	27	10	0	5	3	3
Total	47	1	7	38	0	4	48	17	28	22	26	23
Total	48		7	38		4	65		28	48		23
Total	55			42			93			71		

*Only 11 days were observed and scored in Period 4

PART III: MANIPULATION

Purpose

The purpose was to ascertain the effects on the baseline relationships of the removal and subsequent return of the currently dominant mature male.

Procedure

The procedure was identical to that of Part II, except for removals and replacements of the dominant male. These were as set forth below, and are summarized in Table 1, page 14.

First RK, the dominant male from Period 1, was removed for Period 2. He was caught, placed in a burlap sack as recommended by Sharman and Calaby (1964), and removed to solitude in a room several miles away. He was fed normally except for grass and woodchips, but extra lettuce was given. Period 3 began with RK's return to the living pen. The span of days was extended to 25, for more assurance that the changes in relationships were permanent. In period 4 the now dominant male, Cal, was removed and treated exactly as RK had been. The observations were unavoidably reduced to

10, but the span of days remained 18. Cal was returned at the beginning of period 5 and the span was again extended to 25 days, for the same reason. Period 6 was a removal of the dominant RK for 48 hours, during which no observations were made. His return day was observed, and on several later days sufficient observations were made to ascertain that RK maintained his former dominance over Cal.

Results

Some of the results from Part II are restated below to facilitate comparison with the results obtained in Part III. The scores made during the five main periods are shown in Figures 1-3 and Tables 2-6 but since no change occurred after Period 6 (the 48 hour withdrawal of RK) Period 6 does not appear in the graphs or tables.

Male-male dominance (see Figures 1, 2, and 3, and Table 2, pages 16-19 inclusive).

There were five main results of the RK-Cal composition:

1. that dominance was complete and fixed during the whole of any period except for adjustments during return days;
2. that many dominations occurred in every period;
3. that dominance was reversed by removing the dominant male for 18 days and then returning him, but
4. dominance was not reversed by a 48 hour removal; and
5. that the ratio of unopposed to fighting dominance

was greatly increased when dominance reversals occurred, as compared to the original baseline.

RK-Flo dominance was as follows:

1. RK was completely dominant over Flo throughout all periods.
2. The number of RK-Flo dominations was always a small fraction of the RK-Cal dominations.
3. The number of RK dominations over Flo steadily increased over the five main periods, from 14 in period 1 to 48 in period 5, although period 4 might have equalled or surpassed period 5 if the number of observations had not been curtailed.
4. The ratio of unopposed to fighting dominations increased over the five periods.

Cal-Flo dominance varied with dominance between RK and Cal.

1. In period 1, Cal and Flo had nearly identical domination totals (though in unopposed dominations Cal scored 5 to Flo's 2).
2. When RK was removed in period 2, Cal became very dominant over Flo. Cal's total dominations increased five-fold and his ratio of unopposed to fighting dominations increased markedly, while Flo scored less than in period 1.
3. When RK returned and was subordinate to Cal in period 3, though Cal maintained clear dominance over Flo,

Cal was mostly busy dominating RK. The number of total Cal-Flo dominations shrunk to approximately the level of period 1, and fighting dominance increased relative to unopposed dominance, as compared with period 2.

4. When Cal returned in period 5 and was again subordinate to RK, Cal became slightly subordinate to Flo in unopposed, in fighting, and in total dominance. The total number of Flo's dominations was comparable to Cal's total in period 3, but the ratio of unopposed to total dominance increased and that of fighting dominance accordingly decreased.

Male-female Dominance (see Tables 3 and 4, page 21, Table 5, page 23, and Table 6, page 24.

1. The total number of male-female dominations was a small fraction of the number of male-male dominations (3.4 to 1).
2. Both mature males dominated all females completely, but Del was dominated 65 times to 48 each for Con and Ari, and 38 for Las, when Flo's dominations over females are also considered.
3. Cal's total number of dominations over all females was nearly twice that of RK. Although their totals were rather similar in periods 1 and 5 when RK was dominant, when RK was absent in period 2 Cal's score over females was twice what RK's was when Cal was

absent in period 4. In period 3, when Cal was dominant over RK, Cal dominated females four times as much as did RK.

4. The order of greatest domination of females by RK and Cal together was: Del and Ari (48 and 47 subordinations) followed by Las, 38, and Con 22. (Las was injured midway through period 4 and was hardly ambulatory thereafter, when she had no social interactions at all. The bulk of her dominance interactions were subordinations to Cal in periods 1-3 when he repeatedly attacked her and twice flattened her to the ground with kicks.)
5. Flo's total dominance interactions with females were midway between Cal's and RK's: he was clearly dominant over Del and Con, and clearly subordinate to Ari and Las. Ari expressed this much more than Las, even before Las' injury, perhaps because Flo approached Ari much more than he did Las. Flo's total dominations over Del and Con were only 43. These occurred mostly in periods 1 and 5 when Cal was subordinate to RK. They were far fewer when Cal was dominant over RK, and when RK was absent.

Female-female dominance (see Table 4, page 21, Table 5, page 23, and Table 6, page 24.

1. The total number of female-female dominations (63) was a little over one-fourth the total number of male-female dominations (242).

2. Ari dominated all females in periods 1-4, but was subordinate to Del in period 5.
3. Ari's dominance was expressed almost equally against Con and Del, and far more against them than against Las, even before Las's injury.
4. Ari's number of dominations over females was far the greatest (23) when RK was absent, and second greatest (14) when he was subordinate to Cal--periods 2 and 3, respectively. In the other periods she had much lower totals.
5. Some females had little dominance contact. Over all five periods Las and Del never interacted, Con dominated Del once, and Las dominated Con twice.

Total dominance interactions over the male-male, male-female, and female-female compositions.

1. Males had more interactions than females. The order of greatest number was Cal, RK, and Flo.
2. The female order of greatest number of total interactions was Ari, Del, Con, and Las, with considerable separation between each.

Qualitative Results (from Parts, I, II, and III).

Male-male dominance. These results are divided into return day results and full period results.

Return day results. When RK was returned at the start of period 3, he sat by the West fence alone for a few minutes and then rushed about. Soon all three males rushed in

circles, making it hard to see who chased whom. At first Cal and Flo each avoided several rushes by RK, which was duly scored. Gradually, however, Cal began tentative rushes at RK, in which he flared off to one side when he got within two or three meters. RK followed him a bit at times: yet RK ran once at Flo's approach. After many such approaches by Cal, RK fled and Cal pursued. The chase lasted for some 10 minutes, with pauses. The total score that day was 10 for Cal to 3 for RK (unopposed): and the daily record says, "The scores do not adequately reflect Cal's total dominance now as he chases RK for long periods without pause."

On Cal's return at the beginning of period 5 he seemed to resume complete control, scoring 14 unopposed dominations to 0 for RK; the daily record relates that RK "appears terrified". Yet the following morning RK scored 12 unopposed dominations to 0 for Cal; complete reversal had set in. On both these return days when RK and Cal rushed about after each other, Flo joined in to a lesser degree, appearing to chase whomever was being chased.

The return of the dominant RK after period 6, which comprised a mere 48 hours, resulted in an immediate, prolonged, and uniquely violent battle between RK and Cal. The strength of the kicks drove each animal straight back six or eight feet, several times. Finally, RK kicked Cal utterly flat on the ground twice in succession: the only time such force was ever observed between them. This violent battle greatly

surpassed the frequent vigorous fights (see below) in vigor. After being flattened twice Cal withdrew to a far corner of the yard, leaving RK to copulate with Del, who appeared to be in estrus (see Appendix 5).

RK also dominated Flo, chasing him repeatedly before and after his fight with Cal. Though Flo did not stay to fight, he approached and pulled at Del's head when RK copulated with her. RK could not release Del to chase Flo lest Del escape, as she tried repeatedly to do (and finally succeeded). Observations on several later days indicated that RK maintained his dominance over Cal.

Full period results. For several days after each return day any approach by the dominant male was followed by immediate and rapid retreat of the subordinate (see Figure 4). After about 5 days the subordinate began to fight a bit although, as in period 1, even during these fighting hours a fast two hand grab or nose jab invariably sent the subordinate running without further contact. At other times one mature male, sometimes the subordinate, would slowly approach the other, paws would be raised mutually--sometimes after long hesitations--as though inviting one another to do combat. Many minutes of very slow-motion pawing often preceded a vigorous fight, including kicking (see Figure 5); but sometimes, the pawing died away without a vigorous fight.

Vigorous fighting meant fighting upright (with the metatarsals off the ground), clawing toward the other's

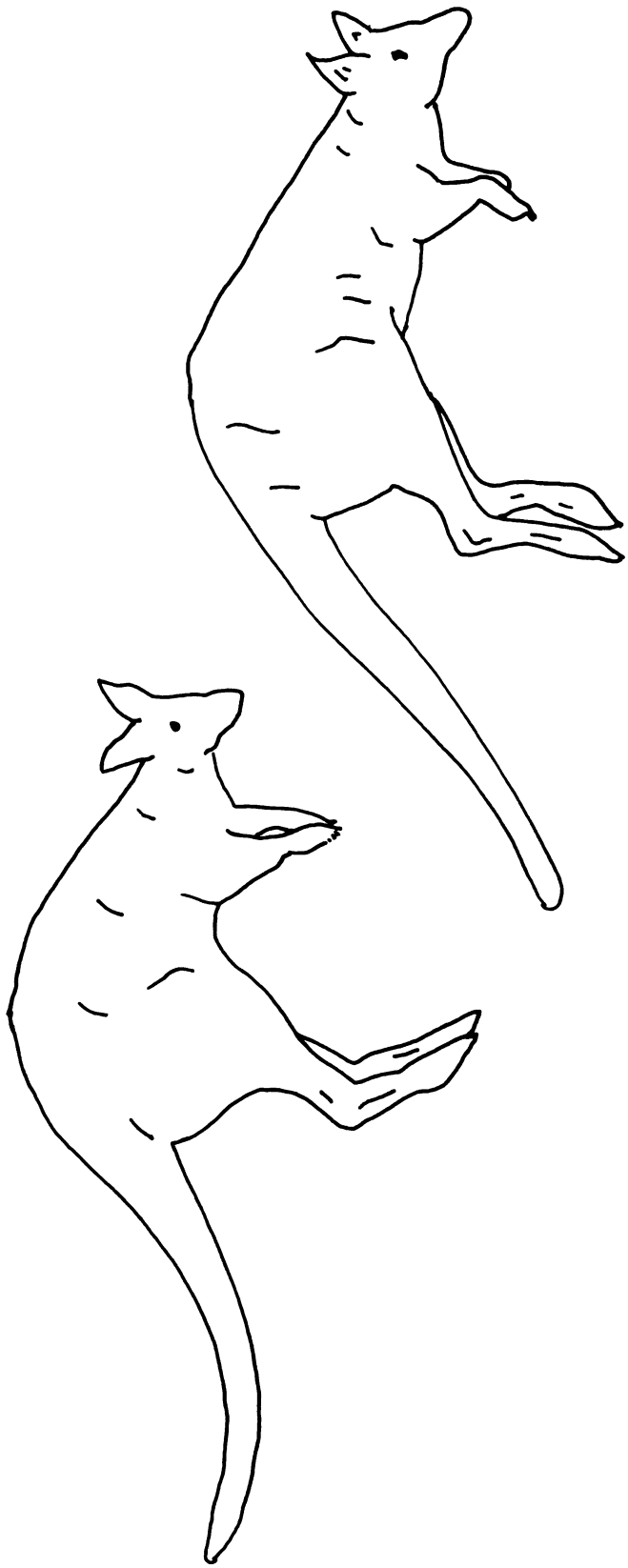

Figure 4. One mature male chasing another.

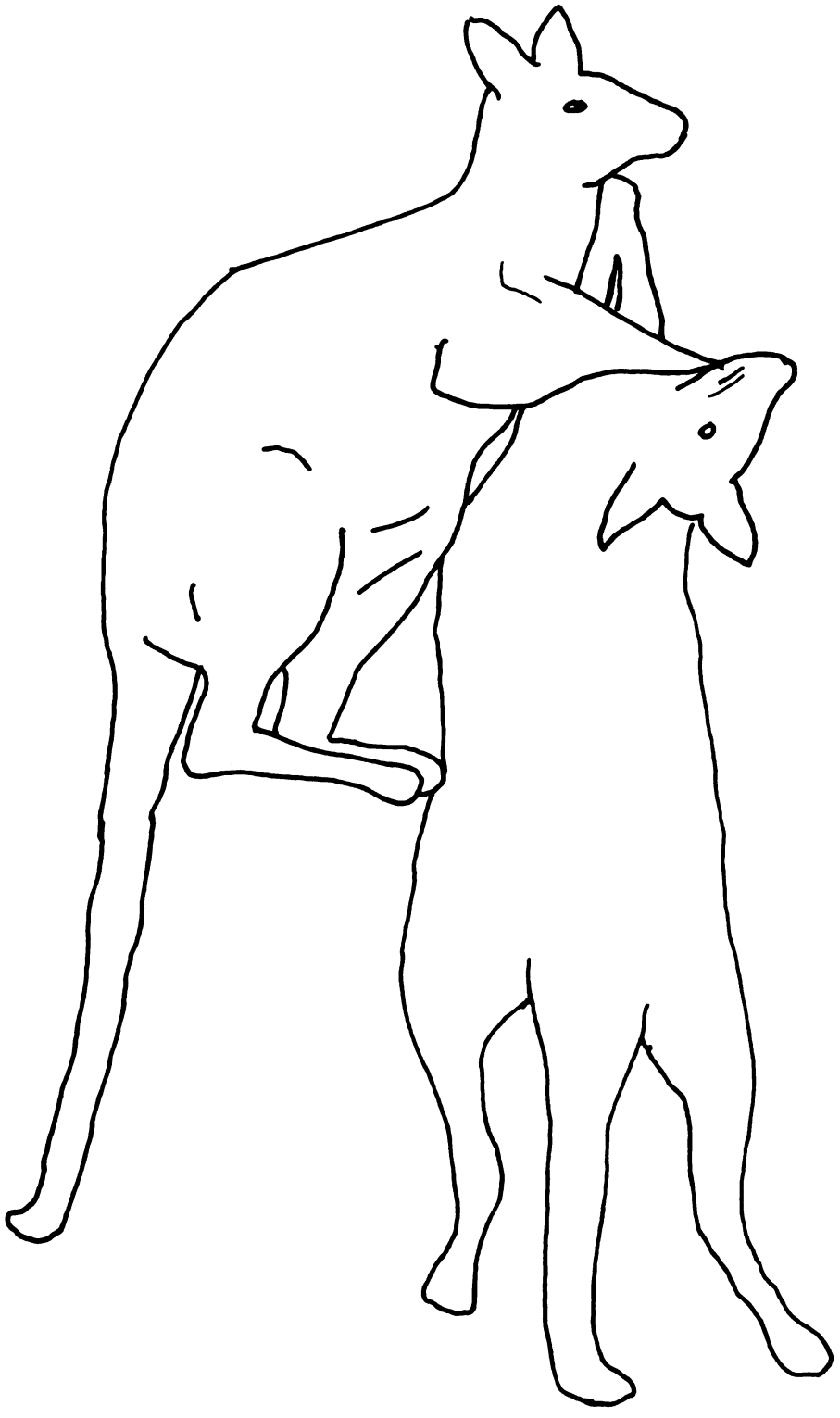

Figure 5. Kick during male-male fight.

eyes (eye-grabbing); pushing against the throat so that the other's head was either forced back or was voluntarily retracted (see Figure 6); wrestling (clasping one another about the shoulders, head and chest and twisting sideways or down in the Greco Roman wrestling manner). Often the subordinate kicked as much or more than the dominant, though there was variation from session to session. However, the subordinate was far more likely to avoid than was the dominant, either by landing in a turnaway after a kick; or simply by a retreat--stepping or hopping away from the fight (see Figure 7). Male-male fights occasionally lasted over 20 minutes, with pauses. Vigorous fighting was always male-male, though not all male-male fighting was vigorous.

Vigorous fighting had often a "king of the hill" quality, with the subordinate sometimes pushing forward harder, backing the dominant male up but not causing him to avoid. Though the subordinate sometimes seemed to fight harder by all the above criteria, in the end he nearly always avoided.

Male-female dominance. Male-female aggression and dominance usually followed male sexual approaches to females. After a female had repeatedly ducked away from grasping male hands, and evaded repeated nosings at her vaginal area, sometimes by hopping away, the male was likely to deliver a two-hand blow, a kick, or a growl plus a chase. Yet is is the investigator's unquantified impression that RK made at least as many advances toward females as did Cal, and was evaded as

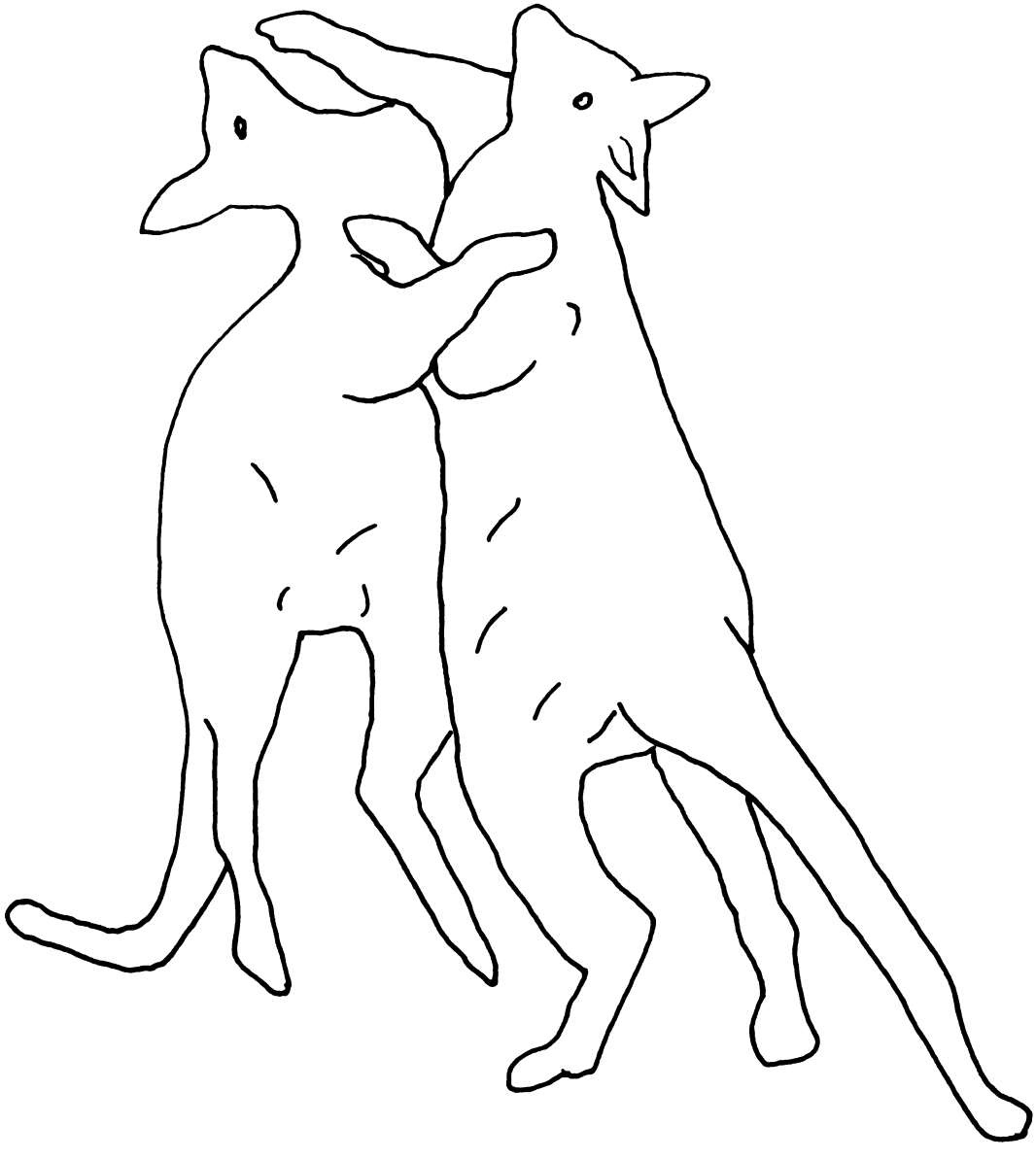

Figure 6. Throat push during male-male fight.

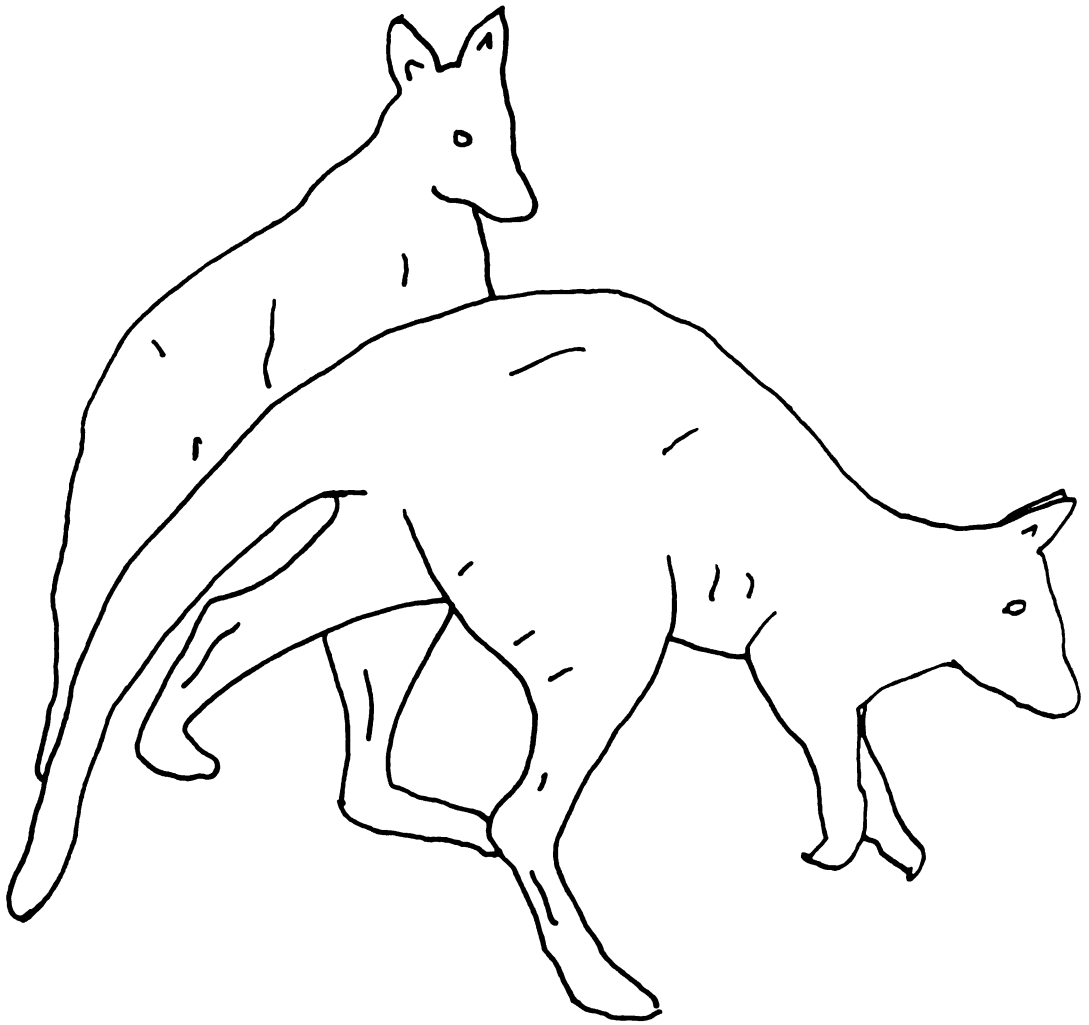

Figure 7. Retreat: one mature male steps away from another during a fight.

often, yet Cal aggressed against them far more, as the quantified results show. Flo's sexual attempts, though also unquantified, were frequent and vigorous, but when he approached Ari or Las, it was they who kicked or grabbed at him. Sometimes Ari attacked Flo as soon as he approached, without waiting for him to nose or paw at her.

Flo's dominations of Del and Con did not differ from those of RK and Cal, except that (very rarely) they fought a bit with Flo before avoiding. Such fights were few, short, and mild. Unopposed dominance was much rarer than in the male-male composition, due to the presence of other behavior classes and the absence of approach-avoidance as an identifier of dominance. Fighting and unopposed aggression were not, therefore, separated for analysis.

Female-female dominance. As with male-female dominance, dominance here was usually preceded by other behaviors: either the nibblings and lickings defined as grooming; or overt homosexual activity such as mounting another female in the male manner; or unclassified pawings. Any of these classes often developed into unopposed or fighting dominance as defined.

Ari's dominance in periods 1-4 (see quantified results) was further shown by her more frequent kickings and blows, both in and out of fights.

Though female homosexuality was not quantified, it was the observer's impression that the dominant females most

often assumed the male role in homosexuality. Ari quite frequently mounted other females. Las made the second largest number of mountings; she showed few heterosexual tendencies, and males rarely showed interest in her (save for Cal's savage aggressions, see Figure 8). Del was never seen to mount another female, and Con mounted Del only once, which was the occasion in the final period previously set forth.

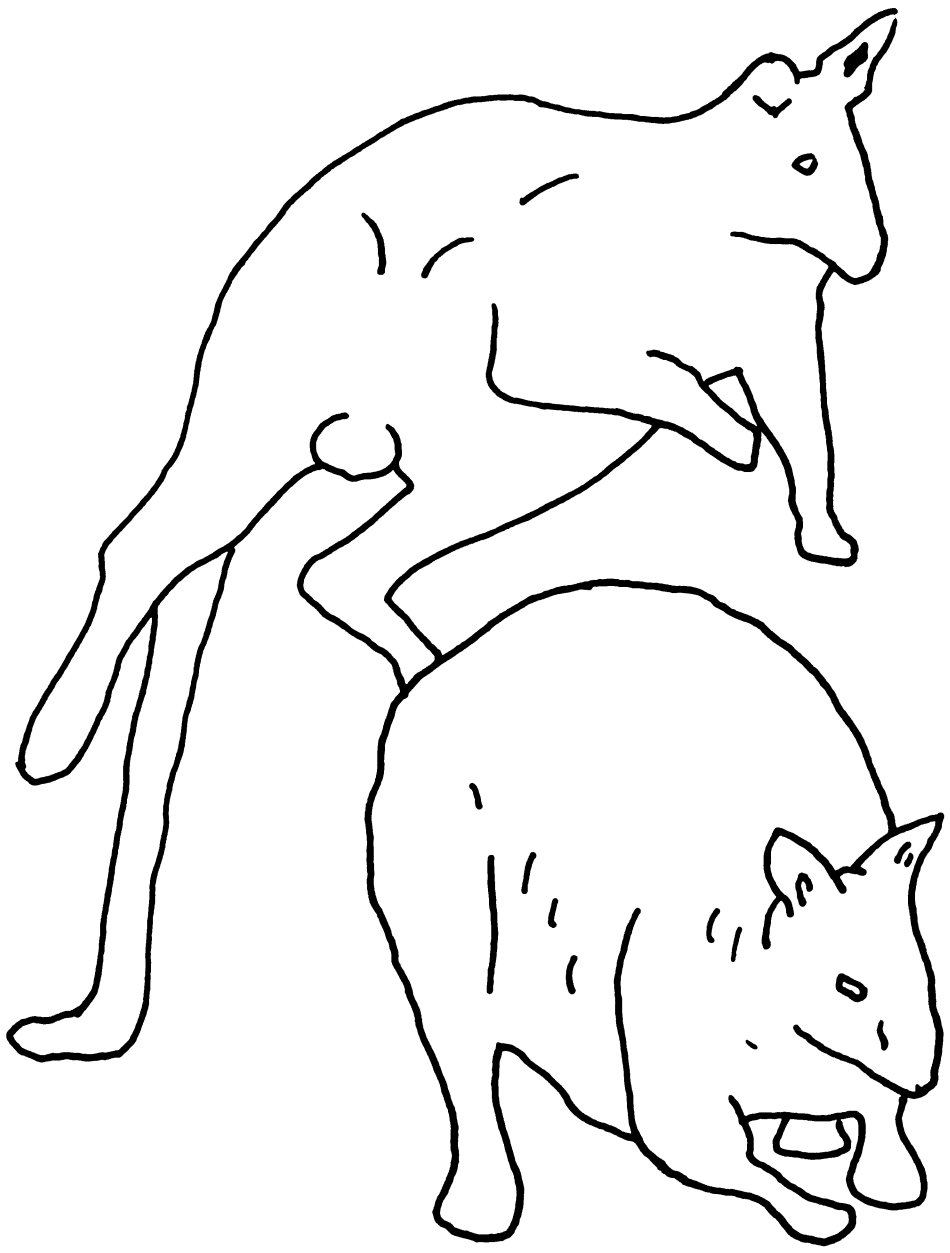

Figure 8. Mature male leaping above female and kicking down at her.

DISCUSSION

A number of questions occur upon comparison of the present results with the meager literature. Any answers are necessarily speculative.

How applicable are the present findings to wild Bennett's wallabies?

It is possible that the dominance types found here exist in the wild also. RK's original pronounced dominance over Cal, which was first quantified in period 1, had been generally obvious and stable during the year-plus that the Ss were at Michigan State. While some of this dominance may have been due to extra aggression stimulated by confinement, the findings of Stodart (1966) and the Breedens (1967) support the existence of dominance in other Macropodids in both confined and wild conditions. Only Stodart considered dominance as such, and she noted that dominations happened frequently, though she made only one count and did not analyze dominance in detail.

Why did the dominance reversals occur?

What makes one animal dominant over another is a complex question, but the present reversal effects indicate that some aspects of the environment are important: one cannot consider

the attributes of the two animals (physical and psychological) in isolation.

Probably the isolation here created mainly psychological factors, but whether it increased the aggressive tendencies of the remaining mature male, or decreased those of the removed animal, or both, is unanswerable; and in any case it cannot be said whether the effects were due to memory failure, to loss of rapport with formerly familiar surroundings and companions, to the trauma of capture, isolation, and recapture, or to some combination of these and other variables. Guhl (1953) points out that with chickens, ". . . a bird fights better in its home area; and . . . even in strange surroundings a bird is more successful when in the presence of its penmates." By moving chickens in and out of isolation, "typically the unrecognized newcomer entered the flock at the lowest rank in the peck order and advanced steadily as new birds were added and resident birds were removed, until it attained top status on its last day in the pen." (However, unusually timorous or aggressive birds were atypical.) In partial contrast, Ginsburg and Allee (1944) found that keeping a mouse in isolation raised its fighting ability. By isolation and gradual, stepped matching they raised the fighting status of timorous mice: the combats were staged in neutral cages. They speculated that isolation might reduce "memory and . . . fear, both produced by previous defeat." Guhl (1953) said that

separation in chickens for two or three weeks results in failure to recognize former penmates. Memory is hard to assess, but behavior on return days at least suggested its presence, for reversal of dominance occurred by degrees, as the return day results demonstrate. And, it seems strained to invoke "forgetting" to explain the violent post period 6 battle, which occurred after a mere 48 hours separation.

Was the violence of the fight on return day 3 due to the 48 hour withdrawal of the dominant male, or to Del's estrus?

The former seems more probable. Since 18 day withdrawals produced dominance reversals, 48 hours of withdrawal may have been a time when the reversal process (whatever its nature) was nearly at the half-way mark, at least in this particular pair of mature males. Perhaps a few more hours of withdrawal would have produced a similarly violent fight, but with Cal victorious. Perhaps too, the withdrawal time needed for reversal depends on the individual characteristics of the withdrawn and of the remaining male.

The exceptional violence of the fight makes it plausible to speculate that such battles occur when, probably rarely, two strange males chance to meet in the wild; or when a newly grown male feels competent to challenge an elder. Nothing of this is discussed in the literature, but it would be interesting to transport males from one mob to another in the hope of seeing such a combat. It must be noted, though, that the extreme lack of social behaviors, except for a vague

general cohesiveness, which was claimed by Caughley (1964) to exist for both the red and the grey kangaroos, and by Kirkpatrick (1966) for the grey, might mean that no battle would develop. Immelman (1965) claimed that Wallabia agilis rarely defends its "home ranges."

However, it is at least possible that the mere presence of an estrual female might provoke such a battle between an already dominant and subordinate male; RK's 48 hour withdrawal should be repeated under non-estrual conditions. Sharman and Calaby (1964) said that they do not keep more than one male red kangaroo with females since one male killed another, but they did not say whether the fight was due to rivalry over an estrual female and whether the males were acquainted and had an established dominance relationship.

What is the function and meaning of the common fights (often vigorous, but not violent) between males with an established dominance pattern?

Such fights may indicate chiefly the revival of some aggressive confidence in the subordinate male after the initial establishment of dominance over him. Even when this revival occurred, the dominant male still exercised frequent unopposed domination over the subordinate, apparently "at will", even during hours propitious to fighting, by a fast nose jab or two-hand blow. Thus the dominant male appeared to permit fights, which seemed to take on ritualistic or even sporting casts. The tentative mutuality with which many fights started, the considerable length of many fights, and the

aggressiveness in fighting often shown by the subordinate male, were in marked contrast to the one-sidedness rigorously maintained in unopposed domination.

Was the ratio of unopposed to fighting dominance a measure of the degree of total dominance between two males?

Yes. The acme of dominance occurred immediately after reversals, when for about five days the subordinate fled at any suggestion of an approach by the dominant. Gradually during this time he fled less; then he began to fight, finally even initiating some battles although fighting never reached the level it attained in period 1, which culminated over a year's dominance stability. So, although the subordinate almost never scored during the fights, standing to fight was deemed to show a lesser degree of subordination than running away.

Is RK a more dominant individual than Cal, other things being equal?

Yes. The only factor suggesting otherwise is that on Cal's return day it took RK longer to take over dominance than it did Cal on RK's return day. However, this may have been due to the five or six humans present on those days. RK was always noticeably shyer of people than Cal, and as Ginsburg and Allee (1942) noted in mice, fear of people is no indicator of inter-animal dominance. Several factors indicate RK's greater dominance, even discounting his initial dominance in period 1 (the reasons for which are undiscoverable); and even discounting his superiority in total

dominance when period 5 is contrasted with period 3. These factors are (1) a higher ratio of unopposed to fighting dominance in period 5 than in period 3; (2) RK's steady and increasing dominance over Flo as opposed to Cal's fluctuating relationship with Flo; and (3) Cal's higher domination scores over females.

As to (1), RK fought with Cal three times as much when RK was subordinate, as Cal did with RK when Cal was subordinate, after the reversals in periods 3 and 5. Items (2) and (3) show that subordination to the other mature male after reversal affected Cal's dominance relationships with other animals far more than it did RK's. RK's dominance over Flo, despite the latter's growth in size and tenacious aggressiveness, seemed completely unaffected by his dominance relationships with Cal, while the extreme change in number and nature of Cal-Flo dominations from period to period suggest that Cal's level of aggression against Flo (a willing contestant for his age) was related to his dominance relationship with RK. Similarly, Cal's relationships with females suggest displaced aggression. Females never fought back to mature males; and when Cal was first free of RK, and then newly dominant over him, his aggressions against the females increased markedly--as if he were drunk with power!

Why were there far fewer male-female than male-male dominations; and far fewer female-female than male-female dominations?

Largely because males had no mutual physical contacts other than aggressive-avoidant, though they did sometimes

graze or rest peacefully in mutual proximity. The other compositions contained the other behavior classes of sexuality, grooming, and unclassified; and their aggression generally evolved from these: it did not appear at once, as in the male-male composition. Male-female aggression appeared to evolve chiefly from frustrated sexuality. Though such frustration was prevalent, since females probably only come into estrus for one day a month (see below), still, females often left before males struck them and aggression was thus avoided. Female-female aggression stemmed only occasionally from grooming or unclassified pawing. It more commonly followed homosexuality, but since this itself was rare, female-female aggression occurred least of all. Dominance was also less common in the non-male-male compositions because they lacked the large category of approach-avoidance in the unopposed avoidance sub-class, which accounted for much of the large male-male totals.

What caused Ari's increase in female dominance in periods 2 and 3, followed by marked decline in period 4 and subordination to Del in period 5?

There is no specific, plausible explanation. The dominance reversal results do not suggest an explanation, whether total RK-Cal dominations over Ari, or their single dominations over her, be considered; nor do her relationships with Flo cast light.

The pattern suggests a cycle--but what? Almost surely female-female dominance does not depend upon estrus, which

probably occurs for one day in approximately a 30 day cycle. Estrus cycles have been studied in Macropodids. Poole and Pilton (1964) found one "exceptional cycle" in one grey kangaroo which lasted 55 days, but estrual cycles for Macropodids generally lasted between 25 and 35 days, with some species having a 5 day variance on either side of their average. Thus unless Bennett's wallaby has an unusually long cycle, its connection with dominance, or with another possibly cyclic factor, female popularity with males, is tenuous.

Regarding popularity, Con was the female least approached by males (except for the abnormal Las) during all but the first days of the quantitative study; yet she was the one most approached during the prior analytical portion, especially by the dominant RK. Male preferences for females would constitute an interesting study.

Though female popularity with males was not quantified as such, the order of greatest domination of females by RK and Cal together (Del, Ari, Las, and Con) gives a limited quantified measure of popularity. Las, however, was not approached sexually; her high subordination score was due to Cal's attacks which were not preceded by sexual attempts. Also, it was the observer's impression that Del was approached substantially more than Ari, but was quicker to leave amorous males before they "lost patience" and struck at her; this deflated her score compared to Ari's.

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APPENDICES

APPENDIX 1

Judgmental Errors: Mistakes Probably Made in Classifying Identifiers Which Were Marginal Between Two or More Classes

Even supposing arguendo that the classes established in the analytical part were adequate and correct, some identifiers sometimes appeared indistinctly, and so were marginal between aggression and some other class. This increased the probability of errors in scoring dominance, especially in the male-female and female-female compositions. Aggressive kicks were marginal with vigorous hops: the pursuer appeared in some rapid chases to kick "tentatively" such that scoring was dubious. Often pawings and blows graded into each other. Rapid pawing sometimes merged into a one-hand blow, though the latter tended to be hooked as heretofore described, while pawing tended to be up and down, though this distinction is not absolute. Fast two-hand blows were quite clear, but slow ones merged easily into pawing, especially sexual pawing of another's rear. In the sexual class the large males sometimes began by pawing and ended with striking when females ducked away from grasping male hands, and even hopped entirely away. Ari and Las sometimes aggressed marginally against Flo when he made sexual advances.

APPENDIX 2

The Goal of the Analysis of Dominance

The goal of the analysis of dominance was "to make the abstract concrete, and the concrete, abstract". That is, to insure that dominance and its components were defined completely but not loosely, so as to contain just sufficient classes and subclasses to particularize dominance according to the compositions in which it occurred. The class of dominance was defined generally as avoidance (a subclass) by one animal immediately after perceiving aggression (a subclass) directed at it by another. The subclass aggression meant either physical attack or threat (behavior which often preceded attack), while the subclass avoidance was non-aggressive behavior which decreased the probability of attack. Both subclasses were essential for the existence of dominance, and were defined as occurring only when certain specifically named and described acts occurred, thus identifying them. Thus in any composition at any time a particular behavior complex should (if the behaviors themselves are distinct and not marginal) either be completely classified as dominance, or completely excluded from dominance, or, if

necessary, considered as still unclassified. Identifiers often differed from the male-male to the male-female and female-female compositions, because the same act might be (say) aggressive in some compositions but not in others. The other classes (sexuality, grooming, and unclassified), were not divided into subclasses for this study and only one identifier was needed to define their existence.

The occurrence of a behavior class was thus made completely dependent upon the occurrence of a defined specific act or acts. Future investigators, either by reviewing the results of this study per se, or by examining in detail aspects which are dealt with only generally here, can then agree or disagree exactly with the class criteria, so that accuracy in classification should increase measurably from study to study. This precise classification properly restricted the traditional criterion for the occurrence of a behavior, that of observer agreement, to the categorization of marginal acts. Though this did not solve the ubiquitous problem of judgmental error, the mis-classifying of marginal behaviors, it at least distinguished it from conceptual errors in classification. Observer agreement should never conceal any lack of explicitness as to which behaviors belong in which classes, given a particular composition or other decisive circumstance. Mistakes of judgment, even mutual ones, must sometimes occur in judging whether act A or act B is transpiring: but given that act A clearly occurs in a

particular composition, then whether it defines aggression, or sexuality, or nothing, should be a matter of previous definition rather than of present observer agreement.

APPENDIX 3

A Further Discussion of the Results of the Analysis of Dominance

Male-male aggression was broadly defined because all the important male-male components appeared to be aggressive-avoidant: either unopposed, or fighting. Dominance in the other compositions was tentatively divided into unopposed and fighting dominance too, but in actual scoring the distinction was not maintained. This was because the borderline between them was fuzzy since the nonvigorous fighting in these compositions often blended with the other classes of behavior they contained and the identifiers were not distinct. Further study is needed here. However, separate scoring was possible in the male-male composition because there was never much physical contact without a fight ensuing; and this separation was desirable because there were so many instances of both unopposed and fighting dominance.

Specifically, successful classification of behavior depended upon the correct selection of identifiers; all distinctions rested upon this. For example, when one male merely approached another directly, the other left so frequently that the sequence was considered to identify

dominance: in particular, unopposed dominance. However, moves merely in the general direction of another male were followed by avoidance much less often, so this was not considered dominance. In the other compositions approaches were never scored because subsequent avoidances were rare and because behaviors other than avoidance often occurred instead. In fighting dominance, mutual pawing identified male-male fighting sufficiently because vigorous fighting, as discussed above, often ensued thereafter and other classes never did. Though males occasionally pawed each other two or three times, or sniffed noses and then separated, this was rare. Usually when one male approached the other either left or stayed and (after some pawing) fought--and then one of them left.

Male-male mutual pawing was therefore deemed unique: sufficient to identify fighting. It did not identify fighting in the other compositions because there it occurred in other classes and subclasses: heterosexuality, homosexuality, grooming, and unclassified, and so it was not unique there. Such mutual pawing often terminated by mutual cessation, or evolved into sexuality, without in either case leading directly to vigorous fighting. Therefore in the latter compositions it could not with reasonable certainty identify any class or sub-class.

The nose jab occurred mostly in male-male unopposed aggression, not in fighting. It was rarely used by females.

Blows, one and two hand, were the commonest aggression form in both sexes. Kicking was rare in male-male unopposed aggression but common in fights; in the other compositions it was common in unopposed aggression and as a terminus to the relatively rare and brief fights. Growling (by either S) plus a chase was the only aggression scored in male-female and female-female compositions in which an attempt to strike was not visible. Growling occurred so often that it was considered an identifier if linked with a chase.

In avoidance, perception of aggression was an essential component. Since approach by one male was so frequently followed by retreat of the other perception of the approach was assumed whenever this happened, unless the S was faced directly away from the approaching S. In these cases the former often appeared to move off casually, frequently to a female: far more often he did not move away at all. Therefore it seemed unwise to assume such a degree of sensory acuteness as to score such rather rare departures as retreats. However, any retreats subsequent to the initial retreat in a series of aggressions were scored regardless of the retreater's head position. After the first retreat he was deemed alerted and his perception was assumed! Since there were so many approach-avoidance sequences in the male-male composition, the probability of a particular avoidance being due to unobserved variables or to chance seemed slight.

In fighting avoidance, the turn-away was an easily observed identifier of subordination. Though the subordinate male appeared to be the aggressor in some vigorous fights his turn-aways always grossly exceeded those of the dominant male. So did his departures by stepping or hopping, but these were sometimes very few till the end of a fight.

Thus various definitions of aggression were required for the sub-classes of fighting and unopposed dominance and for the different compositions, while avoidance criteria were simple and uniform. A special form of aggression, non-avoidance subsequent to a blow or kick delivered by the other S, was needed in the male-female and female-female compositions when the subordinate S sometimes "hit and ran"-- or kicked and ran. Though occasionally in male-male unopposed aggression a blow was delivered without any retreat (this was always between the relatively equi-dominant Flo and Cal) the above hit and run sequence was not noted. See however kicking by the subordinate animal in male-male fighting in the full period results.

Identifiers may require several components for uniqueness, as in the growl plus chase above discussed. Also, some compositions contained several identifiers in one class. For example, male-female unopposed aggression, a sub-class of dominance, was identified by a one-hand blow, or by a two hand blow, etc. But components which occurred solely subsequent to identifiers were not needed as identifiers.

Eye-grabbing was unique to male-male fighting but it occurred only after the appearance of the identifier mutual pawing, so eye-grabbing was not an identifier.

APPENDIX 4

The Existence of Probable Errors in Analysis

Undoubtedly, some errors occurred during the definitions of terms in this analytical period, being either failures to recognize an identifier at all, or wrongly naming non-unique components as identifiers, or mis-classifying identifiers.

Failure to recognize a component as an identifier would conceal the existence of a class, or at least of an instance of it. Perhaps many of the unclassified components contained sub-components or comprised multicomponents which were erroneously unrecognized as identifiers. For example, nosing by a male of a female's vagina area identified male-female sexuality; if a female nosed a vagina, female-female sexuality was identified: but is the very rare male nosing of another male where a female's vagina would be, an identifier of male homosexuality? If so, is homosexuality a very rare exception to otherwise universally dominant-subordinate behavior? Or, should some components concomitant with aggression as defined (such as vigorous fur nibbling during vigorous fighting) be considered as homosexual--or as grooming--rather than as aggressive or unclassified? For the present, it was not considered as an identifier of anything when it occurred

during male-male fighting, though it identified grooming in other compositions. But future studies will doubtless find errors here and elsewhere.

The mistaken recognition of a false identifier would create either a false instance of an actual class, or a false class. Mis-classifying a true identifier wrongly diminishes some counts and increases others. Errors probably increase when several putative identifiers appear simultaneously or in rapid succession. Nibbling, occurring "alone" is a grooming identifier in the male-female and female-female compositions, but it is frequently followed by sexual and/or aggressive identifiers. Does nibbling properly identify grooming, or does it merely identify the onset of sexuality or aggression? Further close study is needed here. Estimation of the relative frequency of occurrence of identifiers and of classes estimated exclusively on the presence of putative identifiers, must often be inaccurate: but this problem should be squarely faced.

APPENDIX 5

Behavioral Evidence of Estrus: Deduced from Reports on Red and Grey Kangaroos

Poole and Pilton (1964) note that in the grey kangaroo "mating usually took place only when the females were receptive"; that is, in estrus. They add that in some cases a male moved to a yard containing females "appeared to over-power the female" and to achieve copulation though she was not in estrus. However, Cal and Flo pursued and clasped at Del with a speed and vigor not previously seen only minutes before RK's return. Also, no copulations had occurred on the other return days which followed much longer absences by the removed male, when he should be more inclined to rape. Captive red kangaroos have reproductive patterns similar to the greys (Sharman and Pilton, 1964). Del's attempts to escape from RK's copulatory embrace need not signify lack of estrus; such attempts were noted in both the above cited studies when the females were in estrus.