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OF COURTSHIP AND COPULATION IN THE GREATER ROAD-
RUNNER (*Geococcyx californianus*-Aves, Cuculidae).

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FIELD AND LABORATORY INVESTIGATIONS OF THE ETHOLOGY OF
COURTSHIP AND COPULATION IN THE GREATER ROADRUNNER
(Geococcyx californianus-Aves, Cuculidae)

A DISSERTATION
SUBMITTED TO THE GRADUATE FACULTY
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degree of
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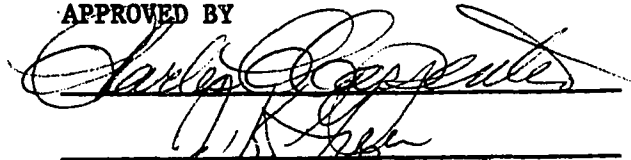
BY
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Norman, Oklahoma

1971

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CHAPTER I

INTRODUCTION

The breeding habits of the avian family Cuculidae are of special interest because of the diversity of breeding patterns exhibited. Represented in the family are social nesting in the anis, nest parasitism in the Old World forms and in one New World genus, and solitary nesting in the New World species. Although information exists on the nesting habits of many of these species, the data on courtship behavior is very meager. A single field observation of copulation (Rand, 1941) and a brief account of breeding in a hand-reared pair (Calder, 1967) represent the information available on the courtship of the greater roadrunner, Geococcyx californianus. Acoustic signals possibly associated with courtship have been described by Holterhoff (1883), Lacey (1911), Dawson (1923), and Sutton (1940) for wild roadrunners and by Calder (1967) for hand-reared roadrunners.

The aim of the present study was to investigate the courtship and copulatory behaviors of G. californianus in both the wild and

captive situations. Specific objectives were to analyze the nature and integration of the various courtship and copulatory behaviors, to investigate the functions of these behaviors, to delineate changes in the courtship patterns with the various phases of the breeding cycle, and to trace the ontogeny of these behaviors.

There is confusion in avian literature regarding the behaviors to which the term courtship refers. For the purposes of this study the definition of courtship as the heterosexual reproductive communication system leading up to the consummatory sexual act will apply (Bastock, 1967). Copulation will refer to the process of cloacal contact.

CHAPTER II

DISTRIBUTION AND ECOLOGY

The greater roadrunner is a ground cuckoo (Family Cuculidae, Subfamily Neomorphinae, Peters, 1940) occurring in the southwestern and midwestern United States and northern Mexico (American Ornithologists' Union, 1957). The roadrunner is generally depicted as a desert species, and recent studies have reported several physiological and behavioral adaptations to desert conditions (Calder, 1968; Ohmart and Lasiewski, 1971). In addition to the desert, however, the species inhabits a variety of habitats throughout its range (Hamilton, 1962; Dixon, 1959; Behle, 1960). It occurs most commonly in mixed, marginal areas of open land and brush or forest, and rarely in the extremes of either sparse or dense vegetation (Grinnell and Miller, 1944). Land clearance and overgrazing with subsequent reinvasion by shrubby species are factors thought to have favored recent range extension (Allen, 1950), which has been considerable for a cursorial form. An eastward movement into Missouri (Brown, 1963), Arkansas (Baerg, 1950), Louisiana (Lowery, 1955), and eastern Kansas (Brecheisen, 1956) has recently occurred, as well as a northward extension along the California coast (Kimsey, 1958).

The diet of the adult is largely insectivorous, but also includes

various vertebrate, invertebrate, and plant species (Bryant, 1916; Gorsuch, 1932). This rather omnivorous diet has also favored range extension. In contrast, the nestling diet is almost entirely reptilian (Finley and Finley, 1915; Woods, 1960). Throughout most of the day the roadrunner is engaged in ground foraging.

The roadrunner is not capable of sustained flight, exhibiting only occasional short, gliding flights. Correlated with its cursorial habit are several myological and skeletal adaptations (Engels, 1938; Berger, 1952, 1954). On the other hand, the zygodactyl foot and the long tail are considered to be adaptations to an arboreal habitat, reflecting the ancestral cuckoo condition (Berger, 1954).

During the non-breeding season the species is solitary. Migration does not occur, and the species breeds throughout its range from mid-March to early September (Bendire, 1878; Sutton, 1940; Prophet, 1957). Double-broodedness has been reported occasionally (Sutton, 1940; Woods, 1960). A variety of nesting habitats are utilized, with the mixed, marginal vegetation again being preferred. The nest may be built from ground level to 12 m or more in various shrub or tree species or on manmade structures (Holterhoff, 1883; Sutton, 1940).

The only other member of this genus, Geococcyx velox, occurs in Mexico and Central America, with the two species being sympatric in portions of central and western Mexico (Blake, 1953).

CHAPTER III

GENERAL FIELD AND LABORATORY METHODS

Description of Study Sites

Field studies were conducted in various sites in Texas and Oklahoma during the summers of 1966, 1967, and 1968, and the springs of 1968 and 1969. These sites are described below with the dates when each served as a study area.

Big Bend National Park, Brewster County, Texas

Site A. Chihuahuan Desert Research Station. 1040 m elevation. Research was conducted at this site from 1 June-10 August 1967, and from 29 February-20 May, 1968. The area around the Station is dominated by broad bajadas sparsely vegetated by creosote bush (Larrea divaricata) and tarbush (Flourensia cernua). Dissecting the plains are arroyos densely vegetated by catclaw (Acacia greggii), lote wood (Ziziphus obtusifolia), javelina bush (Condalia ericoides), desert willow (Chilopsis linearis), and other less common shrubs. An igneous dike also breaks the flat topography and provides erosive slopes vegetated by lechuguilla (Agave lecheguilla), chinograss (Bouteloua breviseta), and desert sumac (Rhus microphylla). This vegetation has greater density and is quite distinct from the shrub-dominated flats and arroyos.

Site B. Panther Junction. 1060 m elevation. Research was conducted at this site 24 July-10 August 1967. This Park headquarters area is on the mid-bajada slopes extending north from the base of the Chisos Mountains. A creosote bush-tarbrush vegetation predominates, with species of the erosive slopes in the previous site being rather common, although more prevalent on the upper slopes of the arroyos dissecting the bajada. The lower slopes and floor of the arroyos are vegetated as at site A.

Site C. Rio Grande Village Campground. 533 m elevation. Research was conducted from 10 March-20 May 1968. The campground area is on the upper terrace of the Rio Grande River floodplain and the vegetation is dominated by mesquite (Prosopis glandulosa), mesquit acacia (Acacia constricta), prickly pear (Opuntia spp.), lotewood, occasionally huisache (Acacia farnesiana), and screwbean (Prosopis pubescens). In the more open managed area around some campsites, cottonwood (Populus spp.) and salt cedar (Tamarix gallica) have been propagated. In previously farmed outlying areas, alkaline flats support four-winged saltbush (Atriplex canescens) and creosote bush, which contrast significantly with the dense floodplain vegetation.

Site D. Castalon-Santa Elena Canyon Road. 646 m elevation. Research was conducted in this area in the summer of 1967 and the spring of 1968. This area, traversed by a 8.85 km road, alternates from the low, heavily vegetated Rio Grande River floodplain dominated by mesquite, mesquit acacia, huisache, salt cedar, and black willow (Salix nigra) to elevated, sparsely vegetated, alluvial plains. The plains are dominated by creosote bush, prickly pear, dogfoot cholla

(Opuntia schottii), and Ocotillo (Fouquieria splendens). Numerous arroyos dissect the flat plains and join the river after likewise dissecting the floodplain. The arroyo bottoms and lower slopes are primarily dominated by the floodplain vegetation and the upper slopes are dominated by lechuguilla, false grama (Cathastecum erectum), various other grasses, and cacti.

South Texas

Site E. Karnes County, Texas. 102 m elevation. A portion of the CO experiment (Chapter X) was conducted in this area on 26 August 1967, and from 23-27 February, 1968. The vegetation of this area is dominated by mesquite, prickly pear, and several short grasses and shrubs.

Site F. Falcon State Park, Starr County, Texas. 79 m elevation. A portion of the CO experiment (Chapter X) was conducted at this site from 21-22 February 1968. The vegetation consists of dense mesquite brush with prickly pear and Spanish dagger (Yucca treculeana) abundantly interspersed. Along the lake shore, huisache is a common low tree.

Oklahoma

Site G. Buncombe Creek Recreation Area, Marshall County, Oklahoma. 197 m elevation. From 10 June-17 June 1966 studies were conducted in this area. The vegetation of the area is a post oak (Quercus stellata)-blackjack (Quercus marilandica)-black hickory (Carya texana) forest. Within the heavily vegetated area, roads, camping, and picnic sites have been constructed, providing numerous cleared areas frequented by roadrunners.

Site H. Willis Cemetery, Marshall County, Oklahoma. 197 m elevation. Research was conducted at this location from 27 June-27 July 1968. The cemetery grounds are bounded by cultivated fields and pastures. Along the fenceline and scattered within the cemetery are post oak, blackjack, elm (Ulmus spp.), cottonwood (Populus deltoides), hackberry (Celtis spp.), and catalpa (Catalpa speciosa). Within the cemetery numerous propagated red cedar (Juniperus virginiana), arbor vitae (Thuja occidentalis), and crepe myrtle (Lagerstroemia indica) occur in the maintained lawn of bermuda grass (Cynodon dactylon).

Site I. Thunderbird Lake, Cleveland County, Oklahoma. 340 m elevation. Research was conducted at this site from 16 May-26 May 1969. The vegetation along the west shore of Lake Thunderbird is a post oak-blackjack-black hickory forest. The forest has been cleared and managed to provide roads, camping, and picnic sites.

Maintenance of Captive Birds

Laboratory studies were conducted from September, 1966-July, 1970 on seven captive birds that were housed in a 9 x 9 x 9 m outdoor enclosure at the Animal Behavior Laboratory of the University of Oklahoma. The enclosure was of 1 in mesh chicken wire except for the west side which was formed by the wooden wall of the laboratory. The enclosure was heavily vegetated with short bermuda grass, a half-dozen scattered small shrubs and saplings (Cornus drummondii, Althaea rosea, Celtis laevigata), and various annual forbs. Numerous perches at various heights were provided as well as a sand-bathing area 1 x 1 m.

A large wooden nest box 29 x 42 x 35 cm was provided near the center of the enclosure at a height of 1.5 m.

The adult diet consisted primarily of whole adult white mice and 1-10 day old baby chicks, with an occasional English sparrow. Supplements of raw beef heart, kidney, and chicken dusted with bone meal and vitamin powder were periodically provided. In addition, the captives caught numerous insects during the spring and summer months. The young birds were similarly fed, but with smaller mice and additional insects.

Observational Methods

Observations made during the study were aided by the use of 7 x 35 binoculars and a 5-60x zoom spotting scope. A blind was not used in the field studies as it would have severely limited the large field of vision needed to observe the active roadrunner, and also would have reduced the vantage points necessary to observe certain behaviors. With only one exception (Site H) the birds readily adjusted to the presence of the observer. Evidence of this adjustment was most striking at Site C, where the adult birds often hopped on the leg or foot of the observer as they approached their nest with food, using the observer as a natural perch. Observations were usually begun at distances of 20-30 m, daily reducing the distance until a final viewing distance of 10-15 m was adopted. Total observation time of breeding behavior in the field was 801 hours. Continuous observations for any one time period varied from a few minutes to twelve hours.

No individual birds were marked during the study to avoid having

the birds recognize the observer as a dangerous aspect of their environment. Most birds exhibited individual plumage variations, usually due to loss of conspicuous feathers, which served to distinguish them. The plumage variation most often utilized was the ventral patterning of the white-tipped rectrices (Fig. 7c).

As the sexes are not dimorphic in the roadrunner, sexual identification was much more difficult than individual recognition. In those pairs observed for extended periods, the sexes were distinguished by behavioral differences, with the final criterion being their relative positions during copulation.

Age distinctions could be made in the field to the extent of determining a juvenile from an adult by careful observation of mouth coloration. It was observed that in the captive birds the mouth was pink for the first 50-55 days of life, then gradually became speckled with black, until 80-85 days of life when the mouth was completely black. This distinction could then be made on wild birds as they fed, panted, yawned, or vacalized.

Laboratory observations were conducted at close range without the use of a blind. Occasionally the observer was from 30-40 m away using 7 x 35 binoculars. Total observation time during the breeding seasons was over 500 hours. Both field and laboratory observations were recorded in a notebook with extensive use of symbols and drawings.

Individual Captive and Wild Birds

Throughout this paper the individual birds observed will be referred to by a symbol. The symbol for each is comprised of letters to denote the following conditions:

<u>State</u>	<u>Sex</u>
W-Wild	M-Male
C-Captive	F-Female
S-Semi-wild	U-Sex undetermined

along with a number to designate individuals. A list of the captive and wild roadrunners referred to in this paper follows.

CM1 was obtained as a 15 day old nestling from Brewster County, Texas, in May, 1968, and was observed in captivity until August, 1970.

CM2 was obtained from site G as a 7-8 day old nestling in June, 1966, and observed in captivity from 1966-1968.

CM3 was obtained from Site G as a 10-11 day old nestling in June, 1966, and observed in captivity from 1966-1968.

CM4 hatched in captivity in June, 1969, and was the offspring of CM1 and CF1. He was hatched in an incubator and hand-reared in isolation from other roadrunners, and observed until September, 1970.

CF1 was obtained as a 10 day old nestling in May, 1968, from Brewster County, Texas, and observed in captivity until August, 1970.

CU1 was on loan from the Dallas Zoo, Dallas, Texas, from 20 May-1 June 1967 and was at least 3 years of age.

CU2 was obtained as a 8-9 day old nestling from Brewster County, Texas, in May, 1968, and observed until August, 1968.

SU1 was obtained as a nestling from Brewster County, Texas, in April, 1968, and hand-reared, but allowed to interact with wild adult and fledgling roadrunners at site A. Its interactions with wild roadrunners were observed until late May, 1968.

WM1 and WF1 were a pair observed at site A during the summer, 1967, as they cared for fledglings.

WM2 and WF2 were a pair observed at site C in the spring, 1968, from the time of pair formation until caring for fledglings.

WM3 and WF3 were a pair observed at site C in the spring, 1968, from pair formation until caring for nestlings.

WM4 and WF4 were a pair observed at site D in the spring, 1968, from the time of pair formation until caring for fledglings.

WM5 and WF5 were a pair observed at site D in the spring, 1968, in the pair formation stage.

WM6 and WF6 were a pair observed at site B in the summer, 1967, from the time of incubation until caring for fledglings.

WM7 and WF7 were a pair observed at site H in the summer, 1968, from the time of incubation until caring for fledglings.

WM8 and WF8 were a pair observed at site A during the spring, 1968, in the pair formation stage.

WM9 and WF9 were a pair observed at site C in the spring, 1968, in the pair formation stage.

WM10 and WF10 were a pair observed at site I in May, 1968, while caring for nestlings and fledglings.

WM11 and WF11 were a pair observed at site G in June, 1967, while caring for nestlings.

WM12 and WF12 were a pair observed at site E briefly during pair formation.

WM13 and WF13 were a pair observed at site E during pair formation.

WU1 was observed at site B in June, 1967.

WU2, WU3, and WU4 were observed in various locations within site D in the spring, 1968.

WU5 was observed at site F in February, 1968.

WU6 was observed at site D in the spring, 1968.

When referring to a breeding pair, these same numerals will be used, such as wild pair 3 or captive pair 1.

Use of Symbols

Symbols for the numerous behaviors and acoustic signals presented in this paper were employed and are listed in the Appendix. In addition, each symbol is explained in the text when it is first presented.

CHAPTER IV

ACOUSTIC SIGNALS

Introduction and methods

Although the acoustic signals of many avian species have been studied with the aid of sound spectrographic techniques in recent years, there is no such study of those of G. californianus. Verbal descriptions of several roadrunner acoustic signals are present in literature (Holterhoff, 1883; Lacey, 1911; Sutton, 1940; Calder, 1967).

One aim of the present study was to elucidate the physical characteristics of the acoustic signals associated with roadrunner courtship by sound spectrographic techniques. Accompanying displays and behaviors related to each signal are presented in Chapters V and VI.

Tape recordings were made of the sound signals of captive and wild birds using a Uher 4000 Report-L portable recorder with a frequency response capacity of 40-20,000 Hz and a Uher omnidirectional microphone with a frequency response capacity of 70-14,000 Hz (manufacturer's specifications). Most signals were taped at a speed of 7 1/2 ips, with a speed of 3 3/4 ips occasionally utilized. The recordings were analyzed with a Kay Electric Company Sona-graph, Model 1029-A, which produces a diagram (sonogram) of the frequency and point in time of each portion of the sound. The wide band filter was used for temporal resolution and the narrow band filter for frequency resolution (Marler,

1969). The frequency band settings utilized and their respective lower and upper effective resolutions are as follows: 20-2000 Hz, 11.2 and 75 Hz; 40-4000 Hz, 22.5 and 150 Hz; 80-8000 Hz, 45 and 300 Hz. Temporal resolutions of the frequency band settings utilized are: 6 msec at 20-2000 Hz; 3 msec at 40-4000 Hz; and 1.5 msec at 80-8000 Hz.

The sonograms were measured to determine the duration of each note of a particular signal, the duration of intervals between notes, and the lower and upper frequency of each note (Marler and Isaac, 1960). Statistical analyses of the data included mean, standard error (SE), and coefficient of variation (CV).

Tape recordings were analyzed by ear for the number of notes in the CO, BR, and CK signals. Duration measures of the WH signal were obtained by timing with a stopwatch while the tape was played at a reduced speed of 15/16 ips.

Each signal was distinguished by an onomatopoetic name, retaining where applicable those names already in use in the literature.

Results

Nine acoustic signals were produced by both wild and captive birds in association with courtship. These signals will be referred to throughout this paper by the following symbols, with the "v" used to distinguish acoustic from other behaviors: coo (vCO), short coo (vSCO), bark (vBR), whine (vWH), growl coo (vGC), single coo (vICO), clack (vCK), whirr (vWR), and pop (vPOP).

All signals but the vPOP and vICO were taped. Numerous recordings of each acoustic signal were made for both captive and wild birds with the exception of vWH which was recorded only for captive birds.

Numerous sonograms were prepared from the tape recordings, with typical wide band sonograms presented in Fig. 1-6. An example of the narrow band and wide band sonogram of the same signal is presented in Fig. 3. Frequency measures from the narrow band analyses are presented in Table 1, and temporal measures from the wide band analyses are presented in Table 2. The next to last column in each table represents the total number of notes analyzed for that signal. Separate analyses are presented for each note of a signal when the sonogram revealed differences, otherwise all notes were combined. Analyses of the CK are presented separately for the sexes as this signal appeared to be different for each sex. With the exception of the vWH, data presented in the two tables represent a combination of wild and captive analyses.

The dominant frequencies for each signal are presented in kHz, the unit most often used in avian literature (Table 1). The dominant frequencies of roadrunner acoustic signals were found to occur below 1 kHz, with the exception of the vBR and vWH, with most signals exhibiting dominant frequencies between .2-.5 kHz. All signals possessed a narrow frequency spread of from .1-.6 kHz. The frequency variability was considerably smaller for certain signals, although this may merely reflect the different sample sizes of notes.

The temporal characteristics exhibited more disparity among the various signals than did the frequency characteristics. The individual notes of signals ranged from means of 80 msec (vBR) to 1.61 sec (vWH), while intervals between notes ranged from means of 23 msec (vWH) to 610 msec (vCK-males).

Table 1. Dominant frequencies of the various roadrunner courtship acoustic signals. Means for maximum and minimum frequencies of each signal are expressed to the nearest kHz.

Acoustic Signal	Mean	SE	CV	Total Notes	No. Birds
vCO-all notes	.5 ¹	.01	16	61	9
	.3 ²	.01	25	61	9
vCO-first note	.5	.02	15	15	9
	.4	.02	23	15	9
vCO-middle notes	.4	.01	27	33	9
	.3	.02	16	33	9
vCO-last note	.4	.02	20	13	9
	.2	.02	26	13	9
vSCO-all notes	.4	.007	4	6	2
	.2	.02	21	6	2
vBR-all notes	1.2	.01	5	32	2
	.8	.01	6	32	2
vCK-all notes	.4	.01	18	38	4
	.2	.006	16	38	4
vCK-males	.4	.005	6	20	2
	.2	.01	18	20	2
vCK-females	.5	.01	11	18	2
	.2	.007	12	18	2
vGC-all notes	.3	.04	29	7	3
	.3	.02	18	8	3

Table 1 (continued)

Acoustic Signals	Mean	SE	CV	Total Notes	No. Birds
vWR-all notes	.3	.01	12	6	3
	.2	.01	14	6	1
vWH-all notes	1.9			1	1
	1.3			1	1
ART-vCO ³	.5			5	
	.3			5	

¹Maximum frequency given in this row.

²Minimum frequency given in this row.

³Symbol for the artificial CO used in the playback experiment.

Table 2. Temporal characteristics of roadrunner courtship acoustic signals. Note lengths and intervals in milliseconds.

Acoustic Signal	Mean	SE	CV	Total Notes	No. Birds
vCO-first note	227	28	43	14	8
vCO-middle notes	448	19	27	39	8
vCO-last note	732	47	24	14	8
vSCO-first note	167	60	71	4	2
vSCO-middle note	286	62	53	6	2
vSCO-last note	1072	25	6	6	2
vBR-note	80	2	22	69	2
vCK-both sexes-note	192	5	22	65	4
vCK-male-note	193	7	20	34	2
vCK-female-note	198	6	19	31	2
vWR-note	634	24	9	5	3
vGC-note	348	9	10	13	2
vWH-note	1609	157	34	12	2
vCO-interval	228	20	37	17	5
vSCO-interval	274	17	18	8	2
vBR-interval	110	5	32	58	2
vCK-interval	487	24	37	56	4
vCK-interval-male	610	25	22	29	2
vCK-interval-female	378	24	33	27	2
vGC-interval	274	19	26	14	2
vWH-interval	231	23	16	4	2

Coo (vCO)

The vCO signal consisted of from 3-8 downward slurring notes (Fig. 1, 2a,b) with the majority recorded (42%) being of 5 notes. Table 3 presents the range and mean number of notes for each bird whose vCO signals were recorded. The captive males possessed signals of from 5-7 notes and exhibited intra-bird variation similar to that of wild birds.

The frequency spread of the vCO was from .5 to .2 kHz (Table 1). Within each note the frequency was slurred downward and also was lowered slightly with successive notes (Table 1, 4). Occasionally, however, the first note of the series was lower in frequency than the second note (e.g. WM4, Table 4). From one to three harmonics were present, ranging upward to 2 kHz. The duration of the note increased with each successive note (Table 2). However, the duration of the interval between notes did not exhibit this trend. In the field this signal was audible at a distance of 250 m, with the middle notes being the most distinct.

Frequency characteristics for an artificial vCO (ART-vCO) used in the playback experiment (Chapter X) are presented in Tables 2 and 4. The first note of this signal was 310 msec and the last note was 740 msec, with the interval between notes averaging 190 msec duration.

Short Coo (vCO)

The vSCO appeared to be a variation of the vCO, but was sufficiently different to warrant a separate category (Fig. 2c, 3). It consisted of from 2-3 notes, similar in tonal quality to the vCO, but with a shorter first note and longer last note than the vCO (Table 2). This

Figure 1. Sonograms of the vC0.

a. Six note vC0 of CM3.

b. Four note vC0 of WU1.

kHz 2 1 0 a



2

1

0



b

2

1

0

Figure 2. Sonograms of the vCO and vSCO.

- a. Four note vCO of WM2.**
- b. Four note vCO of WM3.**
- c. Two and three note vSCOs of WM5.**

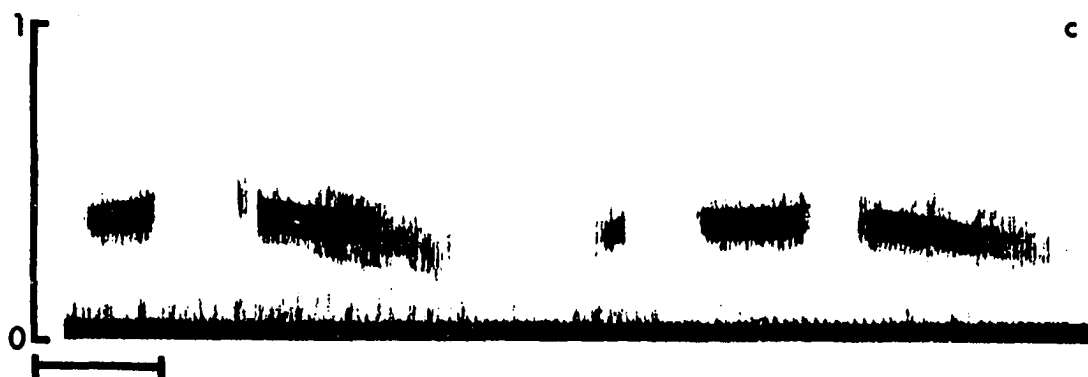
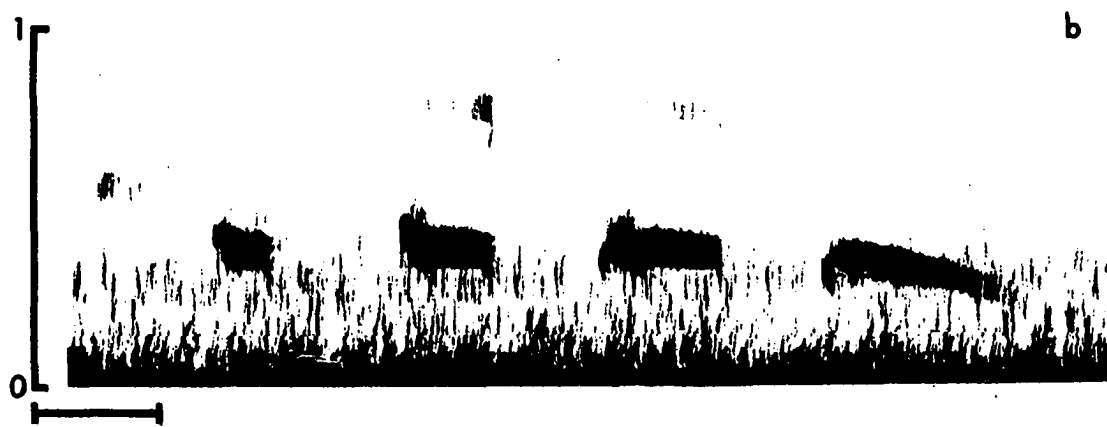
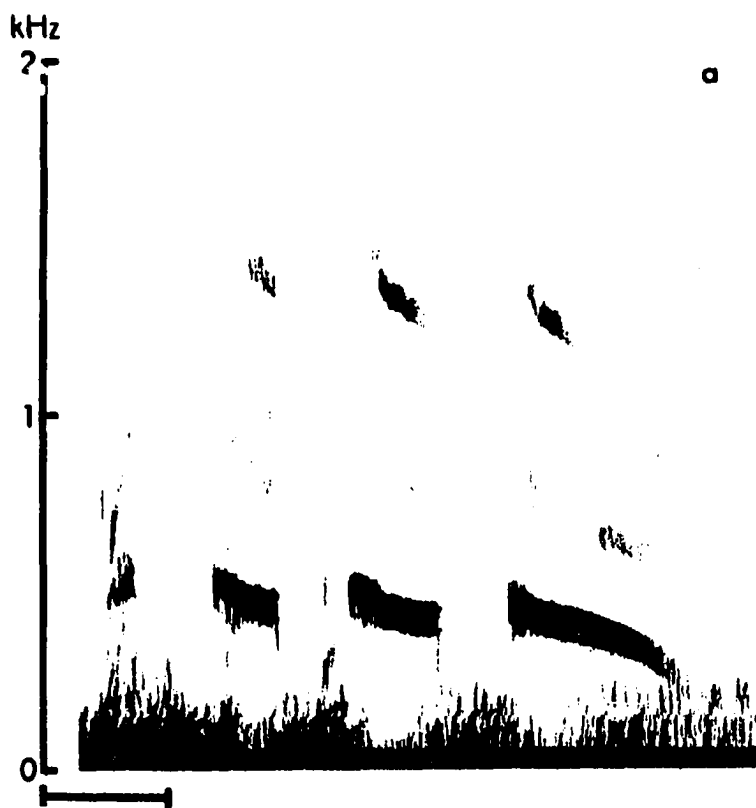


Table 3. Intra-individual and inter-individual variation in the number of notes per vCO.

Individual	Mean	SE	CV	Min No.	Max No.	No. Songs
CM1	6.14	.26	11	5	7	7
CM3	5.90	.23	12	5	7	10
WM1	5.67	.16	9	5	6	9
WM2	4.40	.16	12	4	5	10
WM3	4.92	.31	22	4	8	12
WM4	4.28	.18	11	4	5	7
WM10	5.40	.21	15	4	7	15
WU1	4.83	.40	21	4	6	6
WU2	3.14	.14	12	3	4	7
WU3	4.43	.20	12	4	5	7
All CO signals ¹	5.32	.17	24	3	8	52

¹Based on recordings of 2 captive and 12 wild individuals.

Table 4. Dominant frequencies of successive notes of the vCO signal of individual roadrunners. Maximum and minimum frequencies are expressed to the nearest kHz.

Individual	Note					
	1	2	3	4	5	6
CM3	.5 ¹	.6	.5	.5	.4	
	.4 ²	.3	.3	.2	.2	
CM1	.5	.5	.5	.5	.4	.3
	.4	.3	.2	.2	.2	.2
WM2	.5	.5	.4	.4		
	.4	.3	.3	.2		
WM3	.4	.5	.4	.4		
	.2	.2	.2	.2		
WM4	.5	.5	.4	.4		
	.3	.3	.2	.1		
WU3	.5	.5	.5	.4		
	.4	.3	.3	.2		
WM10	.5	.5	.5	.5	.4	.3
	.4	.3	.3	.3	.3	.2
ART-CO ³	.5	.5	.5	.5	.4	
	.3	.3	.3	.3	.2	

¹Maximum frequency for each note given in this row.

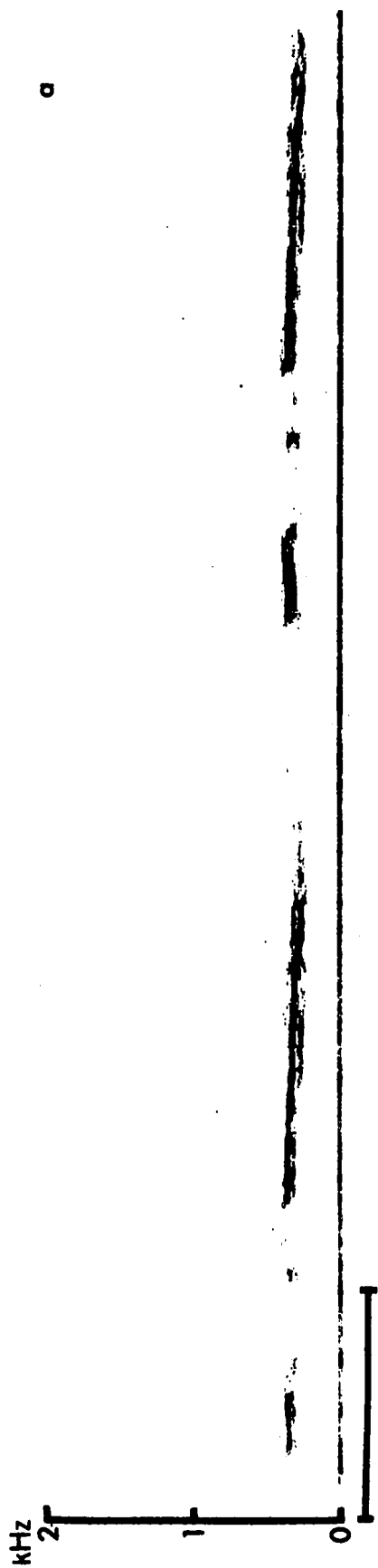
²Minimum frequency for each note given in this row.

³Artificial CO used in the playback experiments.

Figure 3. Sonograms of the vSCO illustrating wide and narrow band analysis.

a. Narrow band analysis.

b. Wide band analysis.



signal was audible at distances of only 30 m or less.

Bark (vBR)

The vBR consisted of a series of identical notes repeated at intervals of 60-210 msec (Fig. 4a). The note slurred upward then downward, covering a frequency range of .8-1.2 kHz (Table 1). This signal possessed seven prominent harmonics ranging from 1-7 kHz and one below the dominant at .2-.7 kHz. The number of notes per signal varied from 2-22 with a mean of 9.17 (SE=.62, CV=54, n=64 notes). An individual bird exhibited a variable number of notes per call, even during one calling session. The duration of the interval between notes averaged longer than the duration of the note (Table 2). This signal was audible to 300 m in the field.

Clack (vCK)

Each note of the vCK consisted of two components, one produced by the mandibles snapping together, while the other originated in the syrinx. In Fig. 5b the noise portion is represented by the regular clicks, occurring in groups of five for each note, and the vocal portion portrayed at the base of the clicks with the dominant frequency between .2-.4 kHz (Table 1) and one or two harmonics at .3 to .4 kHz intervals above the dominant. An average interval of 487 msec occurred between notes (Table 2), while within a note the interval between each click was consistently 30 msec.

As there was an audible sexual difference in the vCK, separate statistics are presented for male and female signals (Table 1, 2). There was a slight sexual difference in note length, but an average of 332 msec difference in the duration of the interval between notes, the notes

Figure 4. Sonograms of the vBR and vWR.

a. vBR of CF1.

b. vWR of CM3.

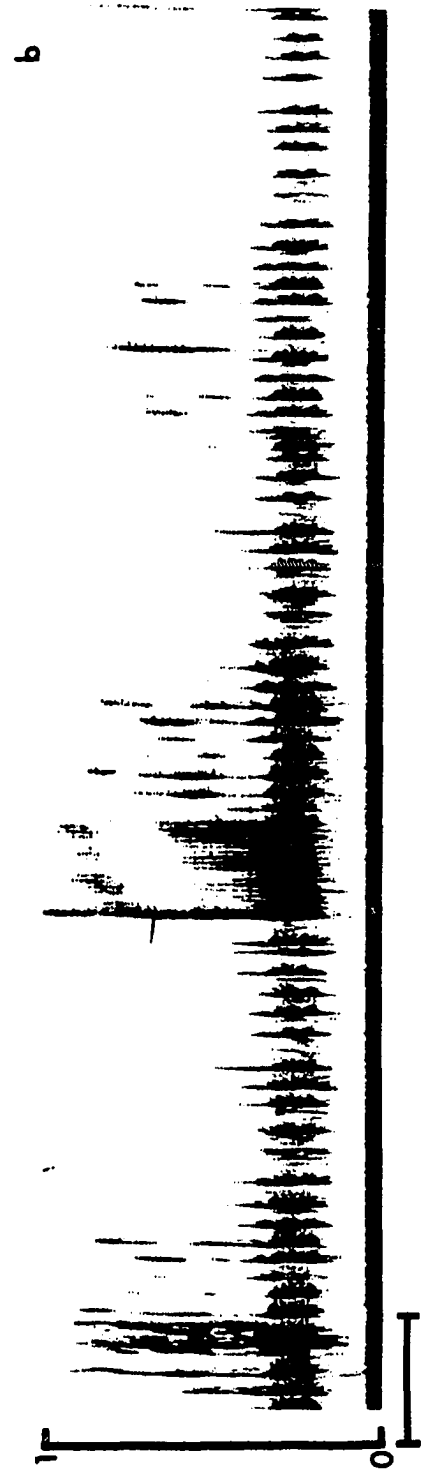
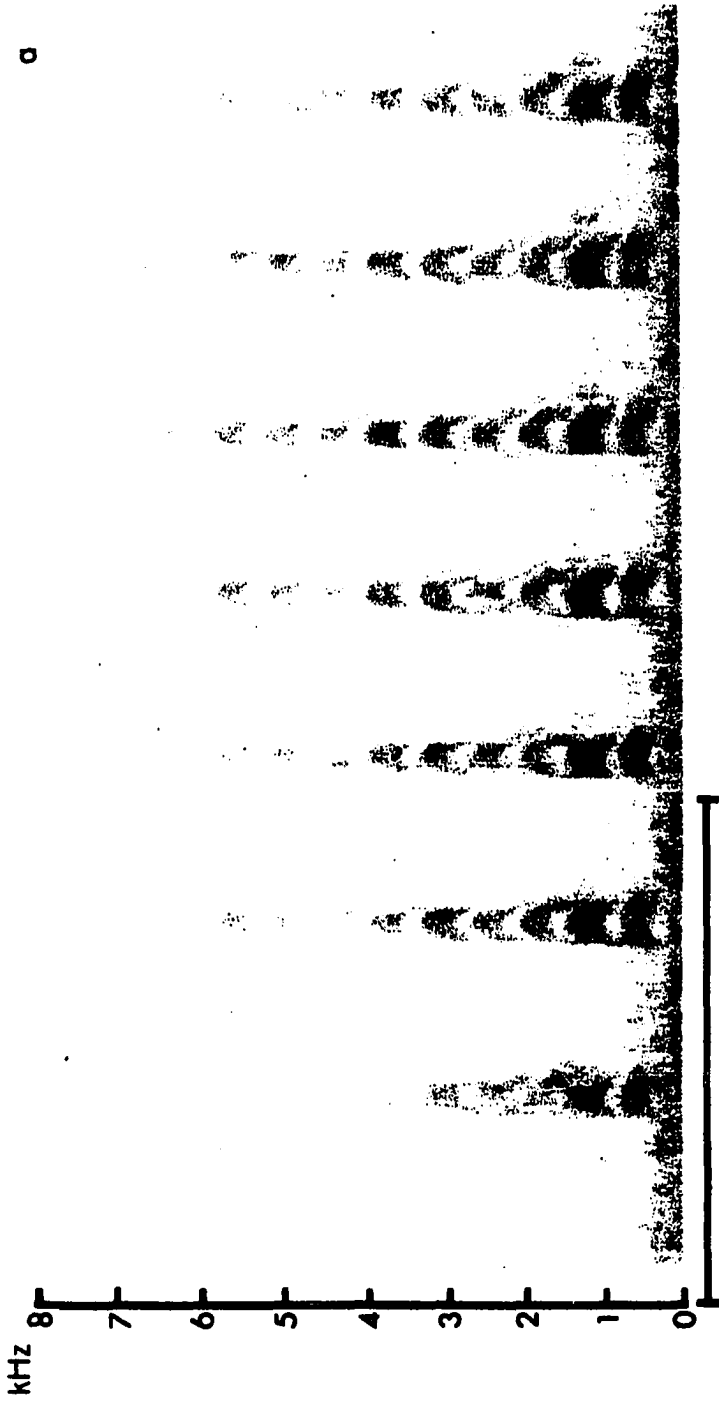
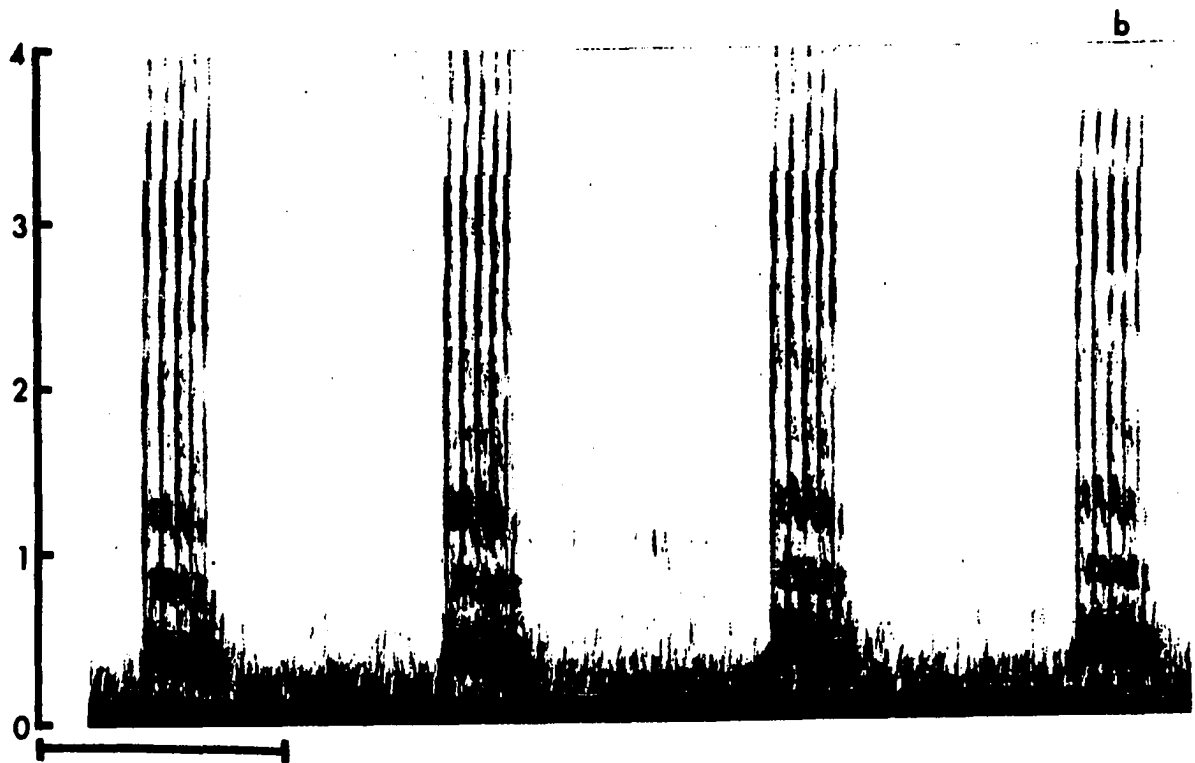
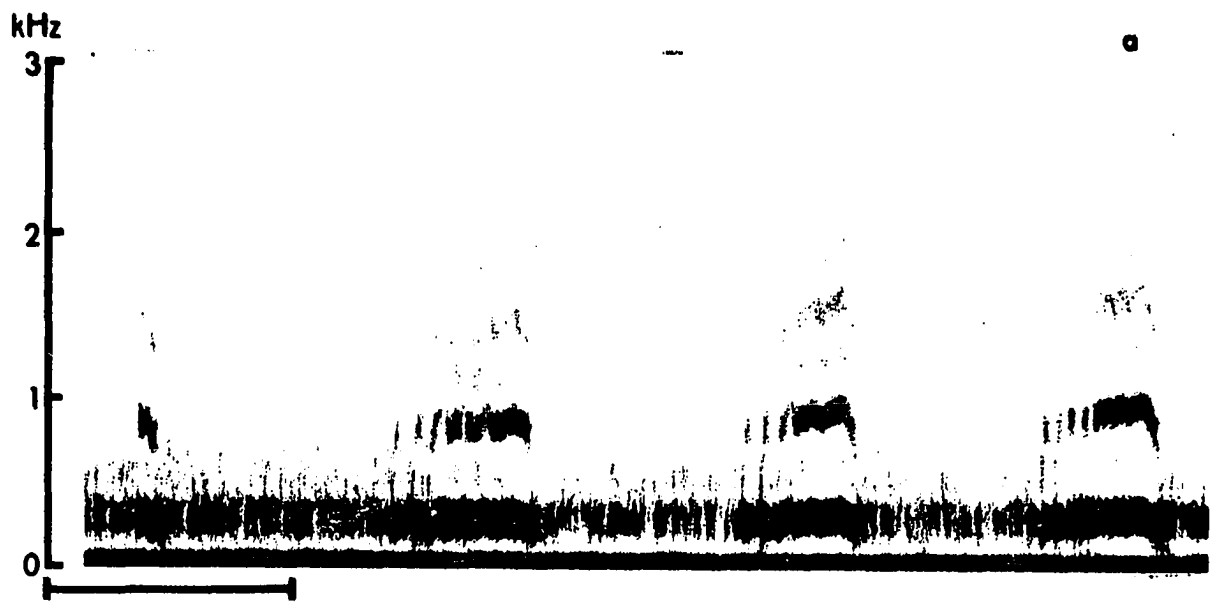


Figure 5. Sonograms of the vGC and vCK.

a. vGC of WM2.

b. vCK of CF1.



of the female occurring closer together. The dominant frequency averaged .1 kHz higher in the female than in the male. Harmonics ranged upward to .7 and .8 kHz in the two males and to .8 and 1.3 kHz in the two females recorded.

The number of notes per signal varied from 1-12 with a mean of 5.67 (SE=.67, CV=64.9, n=30), and one individual would give different numbers in different situations. This call was heard from distances of 50-200 m, varying greatly in loudness with the situation.

Growl Coo (vGC)

The vGC had a dominant frequency of .3 kHz with prominent harmonics at .3-.4 kHz above the dominant, extending to 2 kHz (Fig. 5a). The mean duration of each note was 348 msec with an average interval duration of 274 msec (Table 2). Randomly interspersed between the main notes were shorter notes of the same frequency (e.g. the first note in Fig. 4a). The majority of signals (92%) were of 3-4 notes. As the signal was very soft, it was only audible at distances of 15 m or less.

Whirr (vWR)

The vWR consisted of a series of .2-.3 kHz pulses from 90-150 msec in duration separated by intervals of from 1-120 msec duration (Table 1, 2). Whirring notes, produced by a rapid train of the pulses and averaging 634 msec duration, occurred intermittently (Fig. 4b). The vWR was extremely soft, being audible only at distances of 2 m or less.

Whine (vWH)

The vWH consisted of one long note with a dominant frequency between 1-2 kHz (Table 1) and harmonics at about every .5 kHz above, up

to a maximum frequency of 5 kHz (Fig. 6b). The note was repeated for periods of 1-5 minutes at a time, averaging 231 msec between notes (Table 2). This extremely soft call was audible at distances of 5 m or less.

Although not a courtship signal, the nestling begging call was included in the analyses as its physical characteristics and accompanying behavioral patterns most closely resembled those of the vWH. The dominant frequency of this signal was from .8-1.5 kHz with harmonics to 5 kHz (Fig. 6a). This call was audible at distances of 10 m or less.

Single Coo (vICO)

The vICO signal was produced by both captive and wild birds, although it was not possible to record because of its low intensity and infrequent occurrence. This signal consisted of a single note, similar in tonal quality to one of the first notes of the vCO, but with no discernable lowering of pitch at the end of the note. It was extremely soft, only being audible at distances of 2 m or less.

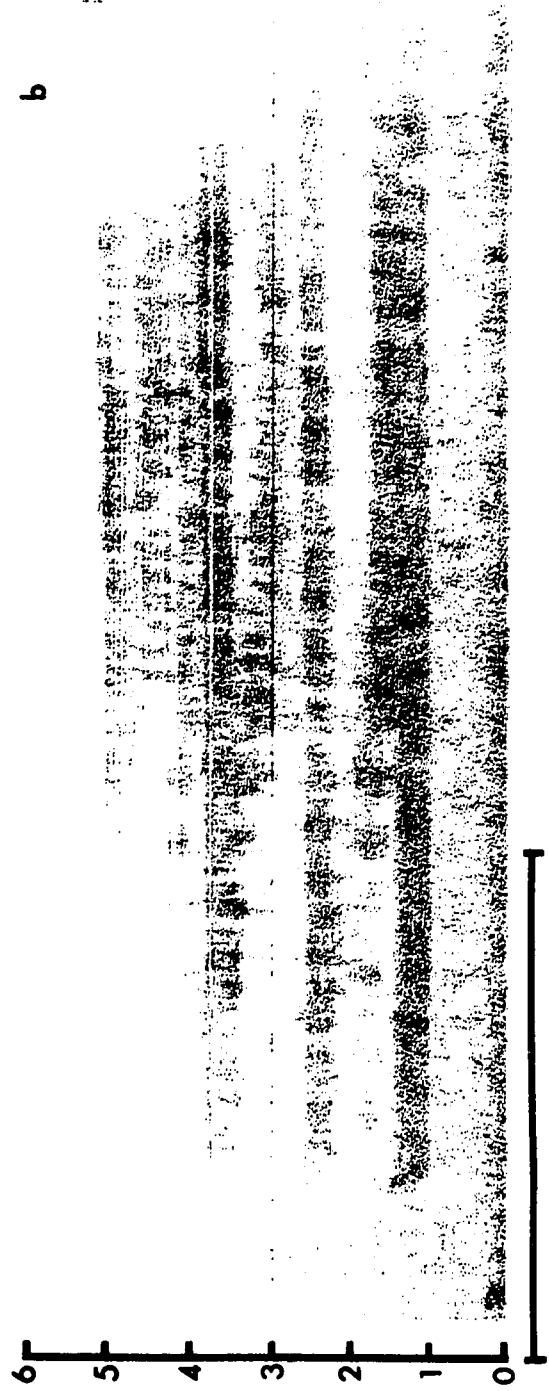
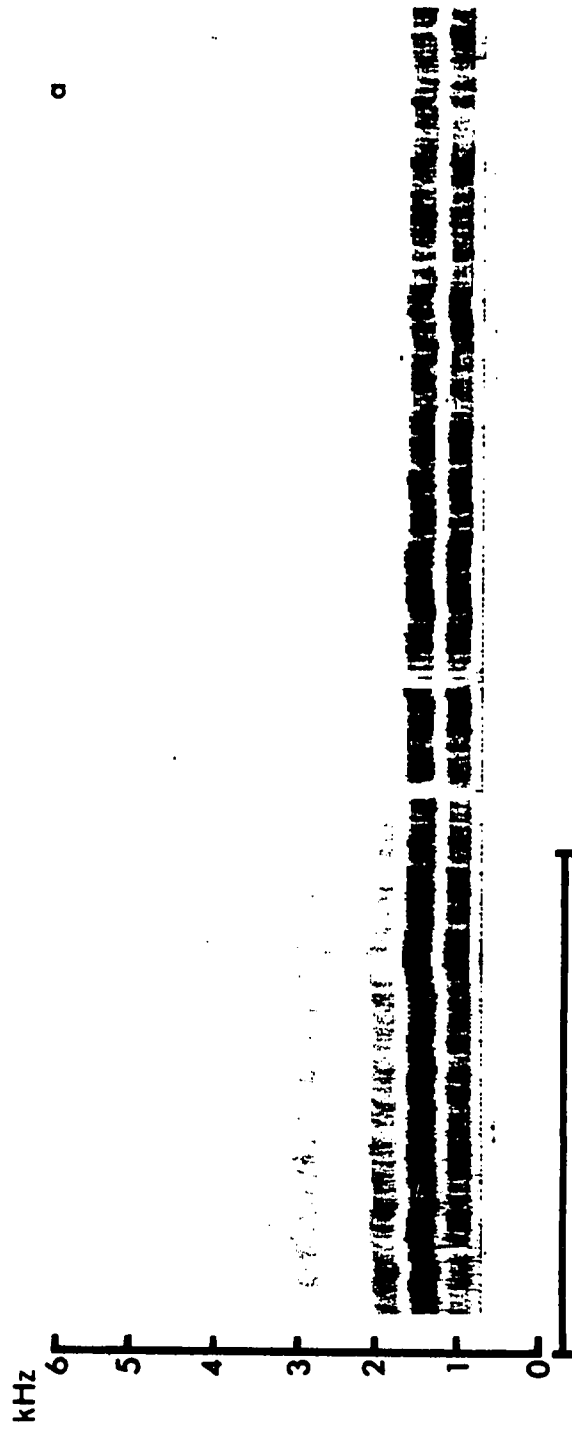
Pop (vPOP)

The vPOP signal was not recorded, primarily because of the unpredictability of its occurrence. It was a series of 4-8 sharp, loud pops produced by the wings being brought inward toward the body of the bird. This signal was audible at distances of 30 m or less.

Figure 6. Sonograms of the nestling begging call and vWH.

a. Nestling begging call of CM1.

b. vWH of CM2.



CHAPTER V

COURTSHIP AND COPULATORY PATTERNS

Introduction and Methods

Observations on both wild and captive roadrunners were made to obtain descriptions of the characteristic courtship and copulatory behavior patterns of the species. Observations were conducted throughout the breeding season and utilized methods presented in Chapter III. Behavioral differences between captive and wild birds were noted for such differences may serve as indicators of the origins of a particular behavior. As behavioral rather than anatomical cues are often used in sexual recognition by non-dimorphic species such as the roadrunner, sexual differences in courtship patterns were of interest in this study. Sexual differences were determined only on birds whose sex was identified by the criterion of position during copulation.

Results

A variety of courtship and copulatory behaviors were observed. The most common behaviors will be referred to by symbols in the remainder of the paper, with the symbol "p" used to differentiate these postural signals from the acoustic signals. The behaviors and their symbols include: tail wagging (pTW), food presentation (pFP), nest material presentation (pNMP), chasing (pCH), flicking (pFK), flicking bow

(pFK-b), postcopulatory display (pPC), and prancing (pPR).

Table 5 summarizes the sexual and wild-captive differences in courtship patterns that were observed. These data are based on observations of wild pairs 1-10, captive pair 1, and captive males 2, 3, and 4, and will serve as the basis for all subsequent statements concerning sexual or wild-captive differences. In considering the quantitative differences presented, it should be kept in mind that each of the wild pairs was observed for only a portion of the entire breeding cycle (Chapter III), whereas the captive birds were observed throughout the breeding season. It is seen that some behaviors were sex-specific, while others were performed by both sexes. The captive and wild birds exhibited similar courtship patterns, with the exception of the vBR given by wild but not by captive males.

Three behavioral patterns were distinguished: preliminary courtship, precopulatory courtship, and copulatory-postcopulatory behavior.

Preliminary Courtship

Preliminary courtship included interactions between the sexes which did not immediately precede copulation. One of the prominent behaviors was pCH, a vigorous ground chase that often lasted for several hours, with both birds stopping frequently to rest. The fast running pace was interspersed with low, gliding flights. Occasionally the pursuing bird would attack the other with wings and tail raised and fanned. As it was not always possible to identify the sexes due to the absence of the copulation position criterion, it is conceivable that some of the chases were of a male-male type. However, the various courtship displays that accompanied the pCH suggested a male-female interaction.

Table 5. Courtship behaviors exhibited by male (M) and female (F) roadrunners in the wild and in captivity. Values indicate number of birds exhibiting each behavior.

Behavior	Wild Roadrunners		Captive Roadrunners	
	M	F	M	F
vSCO	1		2	
vCO	10		4	
pPR	3		3	
pFP	5		4	
pTW	8		4	
pPC	5	5	3	1
pNMP	3	3	4	1
vCK	8	6	4	1
vGC	4	3	4	1
vBR	2	4		1
vWH		4	4	1
pFK	2	5	4	1
pFK-B	2	6	4	1
No. birds observed	10	10	4	1

During the chase the vCK was the most common acoustic signal given by both birds. The pursuing male also frequently gave the vCO, usually from the top of a shrub or small tree. On several occasions the female exhibited vBR while she was the pursuing bird. During the rest stops when the birds were in view of one another, the male exhibited pTW, pNMP, vGC, and vWR, while the female exhibited pFK, pFK-B, pNMP, vICO, and vWH behaviors.

Even though limited by the size of the enclosure, the captive pair exhibited pCH frequently with male and female alternating as pursuer. The male often gave the vCO, while the female frequently gave the vBR. vCK was given by both sexes, but more frequently by the female. Other behaviors accompanying the pCH were similar to those observed in the wild pairs. CM2 and CM3, living together in the enclosure without females, exhibited the pCH as seen in male-female interactions, although no other preliminary courtship behaviors were exhibited to one another. Each would alternate as pursuer, and both gave the vCK during the chasing. CM3 occasionally would chase a human in a similar manner, although this never occurred during the non-breeding season. On several occasions CM4 was released into the enclosure with the captive pair and was vigorously chased by CF1, and rarely by CM1.

Another common preliminary behavior was pNMP, in which one bird approached its mate with a stick or blade of grass in its bill and dropped it a few cm in front of the mate or transferred it to the mate's bill. Often the stick or grass was shaken and thrown down vigorously in front of the mate in a manner similar to that of food treatment in this species. This behavior was exhibited equally by the sexes. Accompanying pNMP by the male were the following behaviors with their

frequencies: pTW, 66.6%; pCH, 37.8%; vGC, 25.2%; vCO, 25.2%. In association with pNMP the female exhibited: vWH, 50.2%; pFK, 37.8%; vGC, 12.6%, pCH, 25.2%. pNMP by the male most often followed the vWH or pFK of the female, while pNMP by the female most often followed the vGC or vCO of the male.

The captive pair frequently exhibited pNMP, with associated behaviors similar to those reported for the wild pairs. The only exception was that of the vWH which was often given by CM1 with subsequent pNMP by CF1. The captive males all exhibited pNMP to humans during the breeding season. When a human was in the enclosure, the male often would pick up a nearby twig or grass blade and bring it to the human. When the human was in view of the captive but not in or near the enclosure, the captive would carry the twig for as long as the human was in view, pacing along the side nearest the human. CF1 was never observed to exhibit pNMP to humans, although she did exhibit the vWH display in the presence of a human and would subsequently accept a twig or grass blade from a human.

The pTW of the male and the pFK of the female, both prominent precopulatory behaviors, were often integrated into the preliminary courtship pattern, but did not culminate in copulation. The male often performed the pTW as he approached his mate during pNMP, but the female gave no overt response to this display, usually continuing to forage, etc. However, she would subsequently give the vWH or exhibit pNMP to him. When the male was persistent, repeatedly performing the pTW around her and attempting mounting, she would exhibit the pFK and leave the area, usually followed at a distance by the male. As he followed, the male gave the vGC, vCO, and pNMP, and the female would occasionally

stop and give the vWH from a bush or tree or exhibit pNMP to him.

The pTW was exhibited by all the captive males. The pTW and pFK were integrated into the captive pair's preliminary courtship pattern as described for the wild pairs. In addition, all captive males exhibited pTW and the associated vWR to humans throughout the breeding season.

The vGC was frequently given by the captive pair throughout the preliminary courtship, especially by CM1 as he pursued CF1. The other captive males gave vGC often.

Although not integrated into the pattern of preliminary behaviors, the pPR and associated vPOP are included as preliminary courtship for they did not immediately precede copulation, except on one occasion (WM2). The pPR and vPOP were exhibited by both wild and captive males in the presence of their mates or to humans.

Precopulatory Patterns

Precopulatory behaviors, those directly preceding copulation by a few minutes, included pTW, pFP, pNMP, vCO, vGC, vCK, and vWR of the male and vCK, vBR, and vFK of the female.

The wild males exhibited the pTW display prior to 69.6% of the 23 copulations observed. Only males that had been paired for some time and were caring for nestlings did not exhibit the pTW. This display was most often accompanied by pFP or pNMP, but occasionally nothing was offered to the female. The items presented by wild males prior to copulation included; lizards, 40.2%; nesting material, 18.2%; snakes, 4.5%; grasshoppers, 4.5%; nothing, 31.2%. Lizard species identified at Sites B and C were: Cophosaurus texanus (Iguanidae), Cnemidophorus

scalaris (Teiidae), Cnemidophorus tigris (Teiidae), and Scleroperus spp. (Iguanidae). Lizards were held by the anterior portion of the body, generally in the foreleg area (Fig. 14), while snakes were looped several times in the bill. Nesting material presented included small twigs (5-8 cm long), salt cedar needles, grass blades, and flower buds.

The acoustic signal consistently preceding copulation was the vWR of the male, given simultaneously with pTW, or, if pTW was not exhibited, as the male neared the female prior to the mount jump. Other male acoustic precopulatory signals with their respective percentages of occurrence included: vCO, 30.4%; vGC, 13.0%; vCK, 8.1%. The female often responded with acoustic signals including: vCK, 45.3%; vBR, 7.0%. Females were never observed to give acoustic signals preceding an unsuccessful copulation, although males' acoustic signals were exhibited equally before a successful or unsuccessful copulation.

As the male approached the female, she would exhibit the pFK display with her posterior presented to the male. The male then mounted with a high (1/2-1 m) jump, landing on her back.

Captive precopulatory displays were similar to those of wild pairs. The pTW was performed consistently by all captive males, but never by CF1. pTW and pFP most frequently occurred at feeding time, for the males would use the mice or chicks fed them as courtship food. A male would often exhibit pTW and pFP for an hour or more before consuming it himself if a human remained in the area. At other times a male would pTW with nesting material or with nothing. The captive males often mounted or attempted to mount a human hand held at ground level. CM1 often alternated his pTW and pFP displays between a human and CF1.

It was difficult to determine if CF1 ever exhibited precopulatory

behavior to the human. She frequently exhibited the pFK display in the human presence, however, this also occurred during the non-breeding season. The pFK by CF1 and mounting by CM1 were similar to those described for wild pairs, as were the precopulatory acoustic signals.

Copulatory and Postcopulatory Patterns

After mounting, the male stood erectly with his feet on the humeral areas of the female as he treaded rapidly, still holding the food or nesting material. The food was held throughout treading and taken from his bill by the female at the time of cloacal contact, although the nesting material was always dropped early in the treading sequence. Immediately following cloacal contact, the male dismounted and circled the stationary female while both sexes exhibited pPC. The male would subsequently exhibit pFK-B occasionally. The female consumed the food after the pPC display, but if there were nestlings, she always fed the courtship food to them.

When copulation was incomplete or interrupted, the male resumed courtship displays, pursuing the female, although copulation usually did not occur again for several hours. Immediately after the twelve unsuccessful copulations observed in the field, the following behaviors were exhibited: males-pCH, 50.0%; pTW, 66.6%; vGC, 25.0%; vCO, 16.6%; and pFK, 8.3%; females-pNMP, 25.0%; pFK, 41.7%; vBR, 8.3%; and vWH, 8.3%.

The copulatory and postcopulatory behaviors of the captive pair were similar to those of wild pairs. The captive males without females exhibited the copulatory treading motions on the substrate beside a human or on the human hand. The cloacal contact movements were fol-

lowed by the male circling the human and exhibiting pPC. CM1 also exhibited treading on the human hand, but did not exhibit the cloacal contact movements or the pPC display.

CHAPTER VI

ANALYSIS OF COURTSHIP AND COPULATORY BEHAVIORS

Introduction and Methods

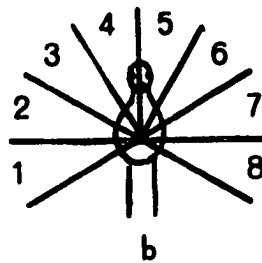
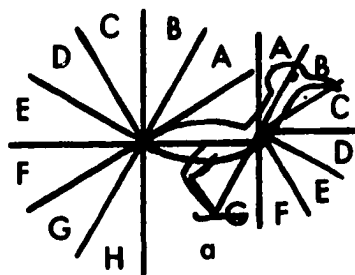
This aspect of the research was directed toward obtaining detailed descriptions of the various courtship and copulatory behaviors of the roadrunner and investigating time-motion relationships of behavioral sequences.

Photographic records of the courtship displays of both captive and wild birds were obtained using a Model H-16 Bolex 16mm movie camera with a 17-85mm Pan Cinor zoom lens. Filming speeds used were 18 and 24 fps with the accuracy of the speed settings checked periodically by filming a stop watch. These films were then projected in slow motion and single frame using a Bell and Howell Model 173 Time and Motion Study Projector. Drawings were produced from the movies by tracing the image on paper, superimposing the image for successive frames. These drawings formed the basis for the time-motion descriptions of behavior, with a temporal resolution of 1/18 or 1/24 sec. Analyses included 4,533 frames of wild bird behavior and 6,520 frames of captive bird behavior.

Certain general body parts and movements will be frequently referred to in the descriptions. For clarity of presentation, these are illustrated (Fig. 7, 8g, 9e) and discussed in the following paragraphs.

Figure 7. Body postures and body parts utilized in descriptions of courtship behavior.

- a. Sectors for head and tail postures from a side view.**
- b. Sectors for describing tail postures from an anterior view.**
- c. Tail in closed position, ventral view.**
- d. Tail in the moderately fanned position, ventral view.**
- e. Tail in the fully fanned position, ventral view.**
- f. Crest normal, post-orbital area obscured.**
- g. Crest sleeked, post-orbital area exposed.**
- h. Crest fluffed, post-orbital area exposed.**
- i. Crest slightly ruffled, post-orbital area partially obscured.**
- j. Crest ruffled, post-orbital area fully exposed.**
- k. Anterior view of j.**
- l. Posterior view of j.**



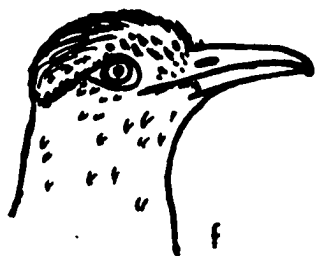
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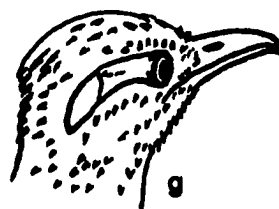
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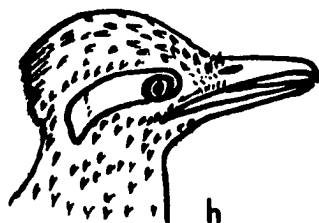
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Tail Positions

The tail of the roadrunner, over half as long as the entire body length, is very prominent, especially when moved. For descriptions of vertical movements of the tail, a diagram, divided into 30 degree sectors, was superimposed on a film tracing and the sector containing the tail was recorded by letter (Fig. 7a). Similar diagrams of tail positions in Pelecaniform displays were employed by Van Tets (1965). Horizontal displacement of the tail (frontal view) was also delineated by 30 degree sectors (Fig. 7b).

The rectrices were spread during certain displays, and Fig. 7c-e presents the degrees of tail fanning. The closed position (Fig. 7a) was the normal tail posture during non-display periods and varied from moderately fanned (Fig. 7d) to fully fanned (Fig. 7e) during displays. During tail fanning the white tips of the lateral rectrices stood out in sharp contrast to the dark plumage of the bird.

Head Positions

Head positions and vertical displacement during display were delineated by 30 degree sectors as for tail positions (Fig. 7a).

Wing Positions

Wing position varied during displays from the normal (Fig. 9e) to drooped (Fig. 8g), to fully fanned (Fig. 8h). During wing drooping and fanning, small white spots on the primaries were exposed.

Post-Orbital Area

The orbital and post-orbital areas are featherless with the orbital area being a pale blue and the post-orbital area a brilliant

orange in both sexes. The orbital area is always exposed, but the post-orbital area is normally completely obscured from view by feathers (Fig. 7f). During courtship the area may be partially exposed (Fig. 7i), exposed (Fig. 7g, h), or fully exposed (Fig. 7j, k, l) as the surrounding feathers are parted.

Crest Positions

The roadrunner possesses extremely fine muscular control of the crest feathers, with their position varying greatly during courtship (Fig. 7f-j). Terminology applied to degree of crest erection follows the feather posture categories of Morris (1956). In the relaxed (normal) position (Fig. 7f), the crest feathers lie loosely on top of one another. In the sleeked position the feathers are closely appressed to the head (Fig. 7g). The feathers are partially erect with tips barely lying on top of one another in the fluffed position (Fig. 7h), while in the ruffled position the feathers are fully erect, with no tips overlying one another (Fig. 7j, l). In Fig. 7i the crest is slightly ruffled. As can be seen for Fig. 7f-l, the exposure of the post-orbital area and the amount of crest erection are independent of one another, contrary to many descriptions in the literature.

General Feather Postures

Contour feather postures will follow the above described terminology of Morris (1956) of relaxed, sleeked, fluffed, and ruffled. When not stated, it is assumed that the contour feathers were in the relaxed position.

Results

The various behaviors are described separately below, and time-motion analyses are summarized in Table 6. Illustrations of the behaviors are presented in Fig. 8-18, traced from the 16mm film. Unless otherwise stated, the descriptions are based on the behavior of captive and wild birds, with no differences being noted between these two groups.

Prance (pPR)

During the pPR display of the male, the posterior view (Fig. 8a) was presented as he ran from his mate or a human (by the captives). As he ran on outstretched legs, the wings were thrown upward to meet above the back of the upward stretched body (Fig. 8e), lowered while held out from the body and drooped (Fig. 8b-d), then brought toward the sides of the body (Fig. 8a). This rapid downward-outward-inward motion resulted in the sharp vPOP noise. The wings were again raised over the back as the bird continued to run, and the sequence repeated for three or four more times. Time-motion film analysis revealed a mean time interval of .43 sec (range .28-.89 sec) between successive wing-up positions (cycles) (Table 6). During the latter cycles the out-in motion of the wings occurred twice before they were again brought up. In all sequences filmed the out-in motion continued for .33-.46 sec after the last wing up position.

The closed tail was held forward (sector A) during the early cycles and gradually dropped to sectors E or F at the end of the sequence as the male ran from the mate or human. This provided a view of the prominent white tail spots which were not visible in the near-

Table 6. Temporal characteristics of courtship and copulatory behaviors of male roadrunners. Time expressed in seconds.

Behavior	Mean/ Cycle ¹	SE	No. Cycles	Individuals
pPR	.43	.01	18	WM10
pTW(with head motions)	.56	.03	59	WM5,2 CM1,3
pTW(without head motions)	.73	.05	44	WM5 CM1,3
pTW(all cycles)	.65	.03	103	WM2,5 CM1,3
Head bow(pTW)	1.43	.20	13	WM2,5 CM1,3
Head lift(pTW)	1.01	.15	13	WM2,5 CM1,3
Head bow-lift(pTW)	2.49	.20	13	WM2,5 CM1,3
Forward head motion(vCO)				WM2,5,10 CM3
First note	.44	.06	12	
Mid-notes	.53	.04	32	
Last note	.83	.16	12	
Forward head motion(vSCO)				WM5
First note	.67	.11	6	
Last note	1.73	.09	13	
Treading	.22	.08	152	WM2 CM1

¹Cycles for each of the behaviors as delineated in the text.

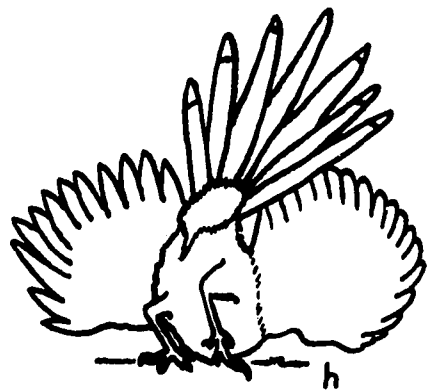
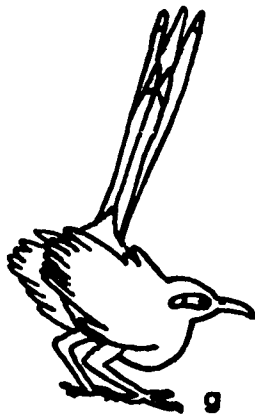
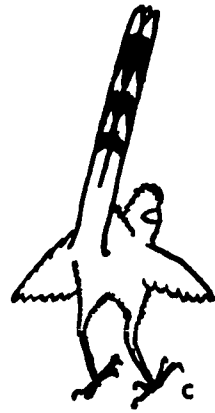
Figure 8. Prance (pPR) display of WM10 and attack postures of WM5.

a-e. Sequence of movements of pPR, rear view (see text).

f. Side view of pPR display.

g. Posture preceding attack.

h. Attack posture.



horizontal, normal tail posture.

During the pPR the post-orbital area was maximally exposed, the crest varied from fluffed to fully ruffled, and the contour feathers were sleeked.

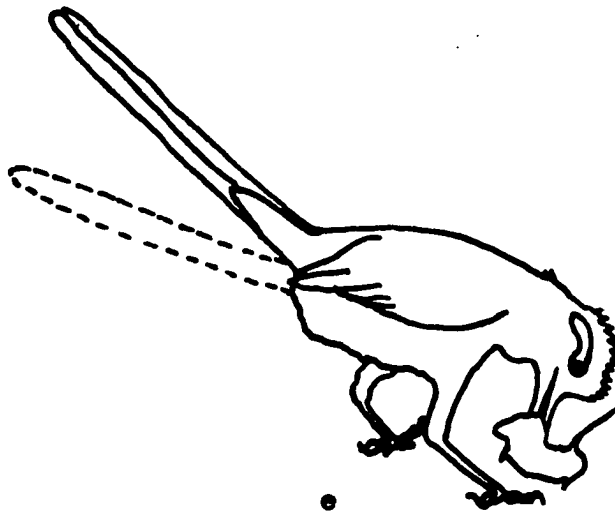
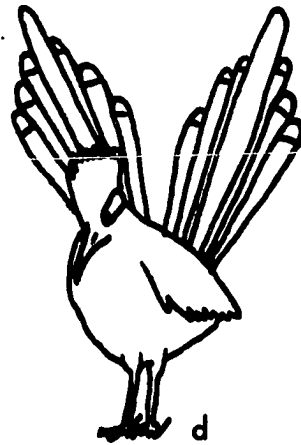
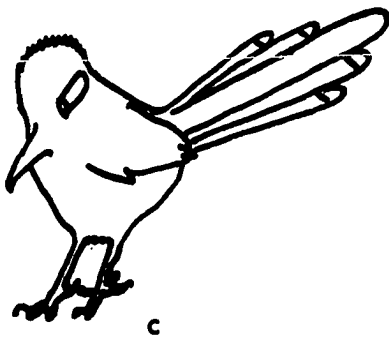
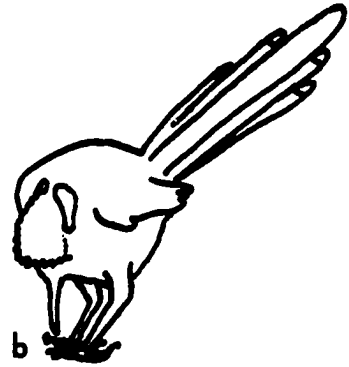
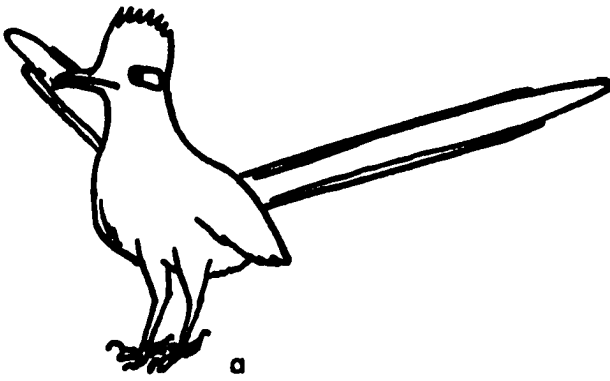
Tail Wagging (pTW)

The pTW involved synchronized tail and head movements, with the basic pattern being a side-to-side tail wagging while the head was intermittently bowed (sector E or F) and slowly lifted (sector B or C) (Fig. 9). When the head was erect during the pTW (Fig. 9a), the tail was closed, however, as the head reached the lowest point of the bow, the tail was fanned and remained fanned until after the head was again raised. The degree of side-to-side movement of the tail also varied with head bowing position. A survey of 118 pTW cycles (a cycle was the horizontal movement from one lateral position to the opposite lateral position and back) for 3 captive and 3 wild birds revealed that when the head is erect, the tail moves from sector 2-7 58% of the time and from sector 3-6 the remainder of the time. When the head is bowed the following sectors and percentages were recorded: sector 2-7, 17%; sector 3-6, 76%; sector 3-5, 2%; and sector 4-5, 5%. The following sectors and percentages were recorded during the head lift; sector 3-6, 66%; sector 3-5, 11%; and sector 4-5, 23%.

The rate of tail wagging was faster during the head bow-lift periods than during the head erect sequences (Table 6). This was expected since a smaller arc was traversed by the tail during the head bow-lift (Fig. 9d). Often the tail wagging halted or slowed appreciably just prior to the head lift (Fig. 9b).

Figure 9. Tail wagging (pTW) display of WM5.

- a. Tail wagging only, showing lateral extremes of tail motion.
- b. Tail fanned and stationary as head bowed.
- c. Tail fanned as head lifted from bow.
- d. Tail wagging continuing as tail lifted, showing lateral extremes of tail motion.
- e. Side view of tail wagging; the dotted line represents the position of the tail as it is swung back in one cycle of the wag.



During the display the male faced his mate, and as the head reached the lowest point of the bow, the fully exposed post-orbital area was in view of the mate (Fig. 9b). The head bowing was consistently slower than the head lifting (Table 6). The crest was ruffled throughout the display.

The vWR (Fig. 4b) accompanied this display, with the slower pulses of the call being produced as the head was erect (Fig. 9a), and the rapid train of pulses produced as the head was lifted (Fig. 9c). The bird was silent as the head was bowing (Fig. 9b).

During the majority of the pTW displays observed in the field and laboratory, the male was holding food or nesting material in his bill, but this did not affect the form of the display nor the quality of the vWR.

Flicking Bow (pFK-B)

The pFK-B involved a bowing of the head (sector D) followed by a prominent throat bulging as the vICO was given, and then a rapid flicking upward of the head and tail (Fig. 15e-f). The entire sequence averaged 2.6 sec in length. The pFK-B closely resembled the pPC (Fig. 15a-d), which was also accompanied by the vICO. The crest varied from fluffed to slightly ruffled, with the post-orbital area exposed or fully exposed and the contour feathers sleeked or relaxed.

Flicking (pFK)

The pFK was a rapid upward flicking of the tail given by the female in conjunction with the pTW and mounting of the male. Analyses of film sequences in which the female exhibited the pFK revealed that two forms were present: those which preceded a successful mount by

the male, and those exhibited in situations where the female avoided the male by moving aside as he jumped.

In the film sequences in which flicks of the former type occurred, the time-motion patterns were almost identical. In the wild sequence filmed WF2 ran in front of WM2, who was exhibiting pTW, stopping in a side-rear orientation 60 cm from him (Fig. 10a). She stood with her tail in sector F, crest fully ruffled, and post-orbital patch exposed. WM2 began his mount .39 sec after she stopped (Fig. 10b). At this same time her tail began flicking upward, reaching sector C at .22 sec after his jump had begun. She remained in this position for .22 sec and then began crouching and lowering her tail (Fig. 10c), but was not in the prone copulation position until .61 sec after the male landed on her back (Fig. 10d-e). The female then slowly sleeked her crest, but with the post-orbital patch remaining fully exposed, and raised her head to just above horizontal and then lowered it to horizontal.

In the captive sequence filmed, CF1 semi-circled CM1, who was exhibiting the pTW (Fig. 11a). As she presented a rear view, she flicked her tail from sector E to C (Fig. 11b). Unlike the wild sequence, however, the male did not begin his mount jump until the female had begun the upward tail flick (Fig. 11b-c). The female then lowered her tail and crouched with head pointing up in sector B as the male landed. As for WF3, the captive female achieved the prone position .61 sec after the male landed and subsequently lowered her head to horizontal.

Several film sequences on both captive and wild females were obtained of the latter situation in which a flick or series of flicks preceded an unsuccessful mount. In these situations the female exhibited a flick that varied somewhat from those given preceding a

Figure 10. Mounting of wild pair 2.

- a. Male (to left) pTW to female.**
- b. Male jumps to mount as female exhibits pFK.**
- c. Female lowers tail and wings as male above her in jump.**
- d. Male lands.**
- e. Female lowers to the substrate as treading begins; her tail is the upper one.**

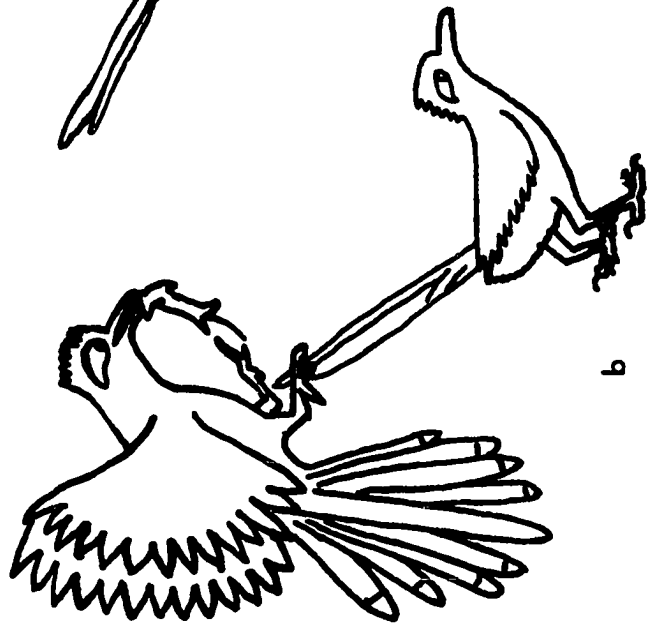
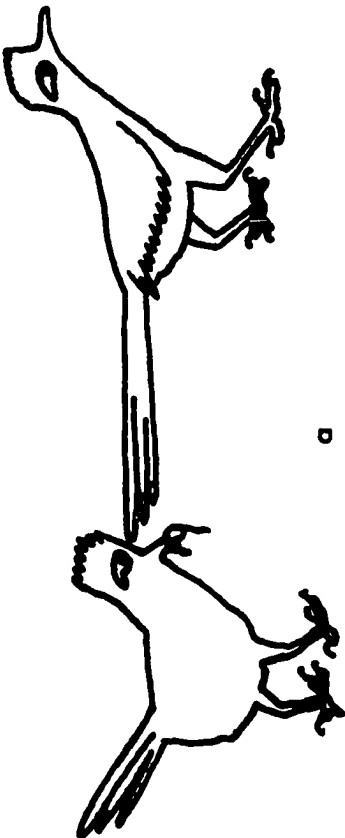


Figure 12. Flicking (pFK) of CF1 as CM1 pTW preceding an unsuccessful mount attempt.

- a. Female stops as male (not shown) pursues and tips her tail toward him.
- b. Female jerks tail up and to side away from male.
- c. Female continues rising tail to upward, central position.
- d. Female begins lowering tail and leaves area as male (to left) approaches.

Figure 11. Flicking (pFK) of CF1 as CM1 performs pTW preceding a successful copulation.

- a. Female presents a side view to male (shown with food).
- b. In the same location the female turns her rear to the male and flicks her tail up.
- c. The male begins a successful mount jump.



successful mount, although it was similar in both captive and wild females. Fig. 12 presents a sequence exhibited by CF3. The female, pursued by the male, stopped 2 m from him, dropped her tail (sector F) and tipped it toward him (Fig. 12a), and then rapidly jerked it upward, away from him (Fig. 12b). It was then lifted to sector C, providing a rear view to the male similar to that presented preceding a successful mounting (Fig. 11b). She then moved away, lowering her tail to sector D as the male approached (Fig. 13b). The entire tail lift from sector F to C took .22 sec.

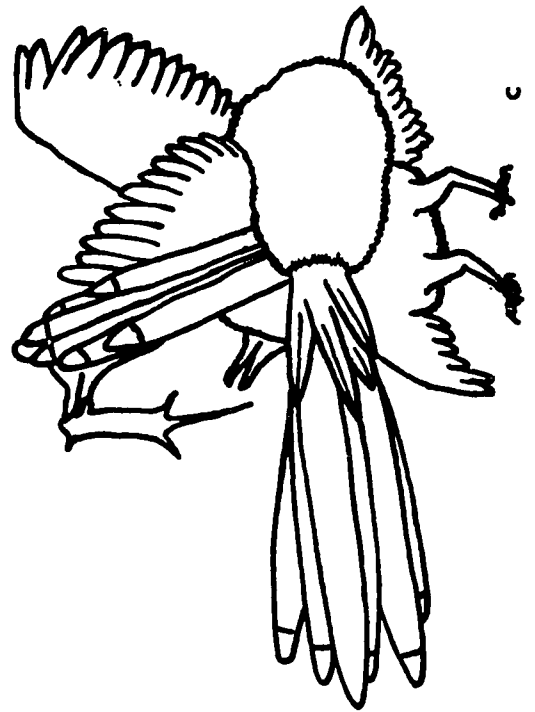
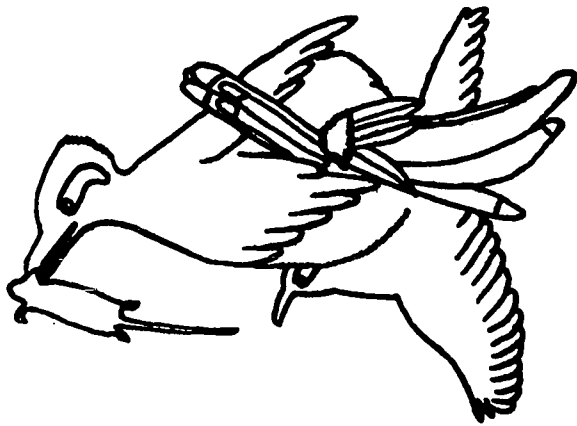
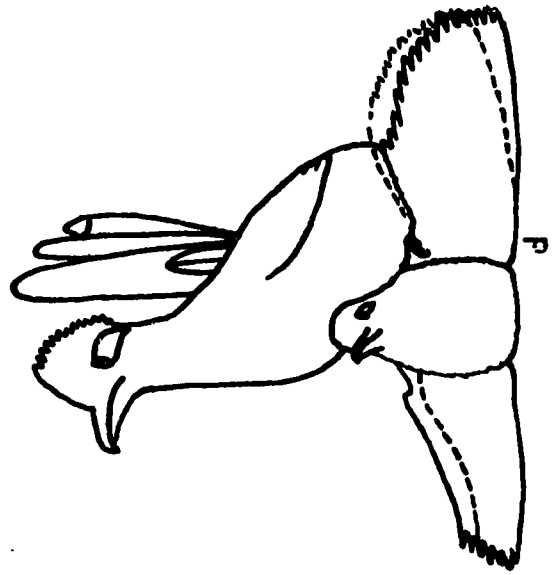
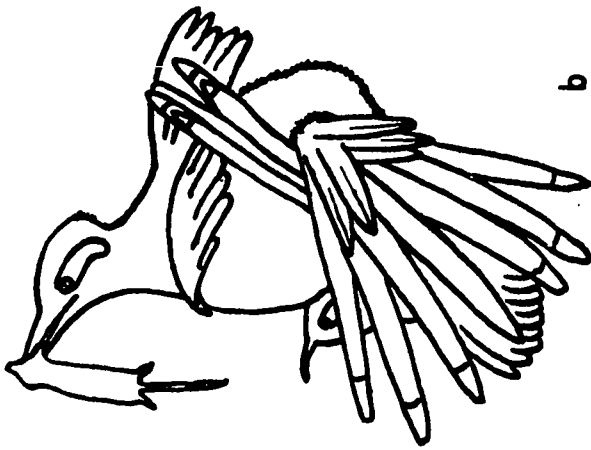
The major differences between the two types of flicks were the extreme closing of the tail and its initial sideways movement in the latter type. In both the wings were flicked down and slightly out as the tail began the upward flick, however, these movements were more obvious in the latter type.

Mounting Jump

The male mounted the female from the rear with a high jump of .5-1 m. WM2 accomplished the jump in .78 sec. As he began the jump, the male's wings drooped slightly and the tail was closed, while at the summit of the jump the wings and tail were fully fanned (Fig. 10b). While descending, rapid wing flapping and maximum tail fanning occurred; and after landing, three or four additional wing flaps were given, apparently to aid in balancing (Fig. 10d). His crest was fully ruffled and the post-orbital area fully exposed during the entire jump. The captive males performed a similar high jump with the rapid wing flapping and tail fanning as they mounted the human hand, even when held at ground level.

Figure 13. Copulation of the captive breeding pair and wild pair 3.

- a. Treading early in the sequence; male's tail is underneath.**
- b. Treading just prior to cloacal contact.**
- c. Cloacal contact.**
- d. Anterior view of treading by WM3; dotted line indicates changes in female's wing position as he treads.**



Copulation

As the male treaded, the female's body was oblique to the ground with her breast feathers just touching the substrate and posterior highly elevated, supported posteriorly by her legs and anteriorly by her outspread wings (Fig. 10e, 13a). Her tail was closed and held in sector D, while the crest was sleeked and the post-orbital area exposed to partially obscured.

The male treaded as he stood erectly with one foot supported by the humeral area of each of her wings (Fig. 10e). Initially, his tail was held in sector F (Fig. 10e), then raised to sector D or E (Fig. 14g), then gradually lowered to sector G at ground level and fanned as the tail and posterior body moved from side to side under the upraised tail of the female (Fig. 13a). In the early treading stages the male's crest was fully ruffled, but it became sleeked as treading proceeded. The post-orbital area was fully exposed throughout the sequence.

With each foot tread the female's wing was displaced vertically (Fig. 13d). This displacement was utilized to measure the treading rate, with one cycle defined as the rise and fall of the wing to the original position (Table 6). The treading rate in CM1 and WM2 averaged .22 sec per cycle with rates early in the sequence slower (range .30-.34 sec) than those later in the sequence (range .18-.23 sec). Near the time of actual cloacal contact the treading rate always increased rapidly, and the male's tail swung further to the side of the female, rubbing against her cloacal region (Fig. 13b). Shortly before cloacal contact the male's crest became sleeked and he began wing flapping, apparently to aid in balance and positioning during cloacal contact.

Duration of treading sequences was not accurately measured, but estimates were from 2-3 min.

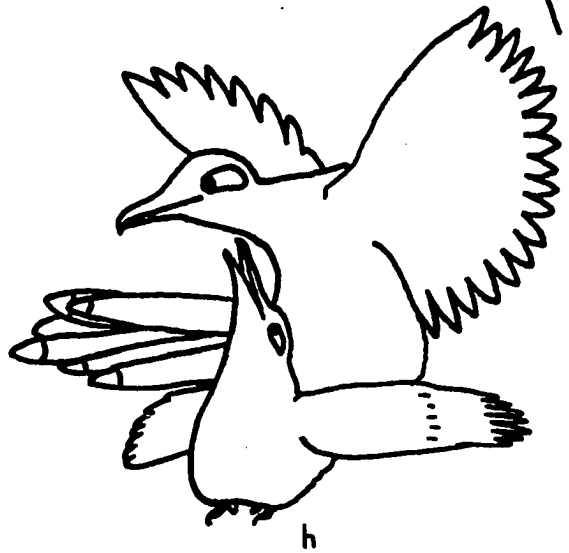
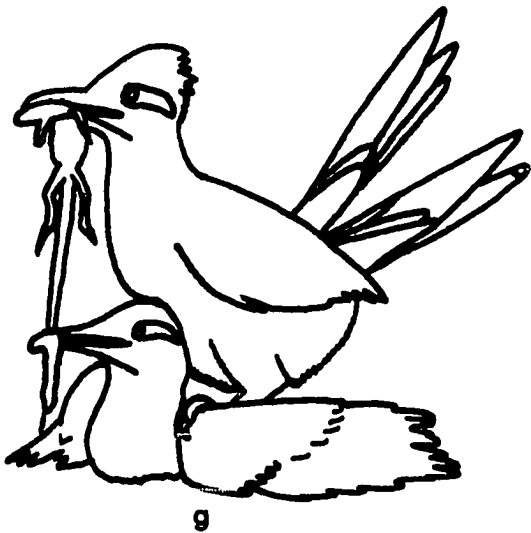
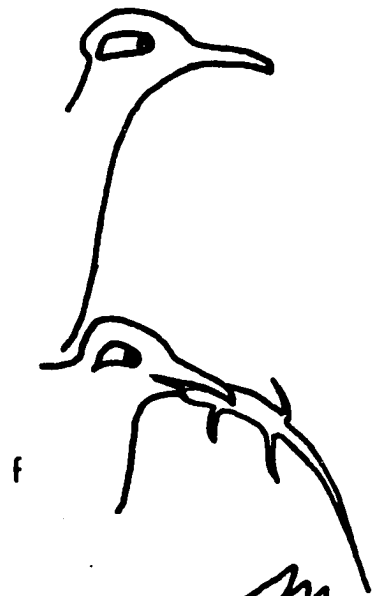
The cloacal contact occurred as the male's tail swung forward and upward (Fig. 13c, 14h) and lasted for .11-.17 sec, as the tail was held in this position. At the same time the female rose slightly from the substrate and lifted her head upward for the food item. These upward head movements of the female occurred even in cases where the male had no food item (Fig. 14h), or when the female already held food for the young (Fig. 14g). As she grasped the food item, the male's head lowered slightly (Fig. 14a-f). Whether this lowering was an active or a passive movement could not be determined from the film. Both mutually held the food item for an average of .28 sec ($SE=.05$, $n=4$) before the male released it.

During food exchange the female's tail was in sector E and the male's tail in sector D. Her post-orbital area was partially obscured, while his remained fully exposed. The male dismounted .42 sec ($SE=.05$, $n=5$) after he released the food item. Upon dismount his tail was in sector E, while hers was in sector B. The crest of both became fluffed.

CM2 and CM3 would tread on a hand held at or near ground level. The films depict their treading postures and tail motions to be identical to those of wild males. Although cloacal contact, tail motions, and wing flapping were exhibited, no evidence of ejaculation was seen. Treading in these males often lasted for 10 minutes or more. Food items were held by the captives while treading, although the item was not released during the cloacal contact motions. It continued to be held during the pPC display and was subsequently eaten by the male.

Figure 14. Food exchange during copulation.

- a-f. Exchange of lizard; wild breeding pair 2.**
- g. Copulation as both sexes hold food intended for nestlings; wild breeding pair 2.**
- h. Copulation with no food exchange occurring; wild breeding pair 2; note position of female's head.**



When an attempt was made to remove the food from a captive male's bill as he treaded, slight force was required, supporting the view that he was a passive partner in the food exchange. Although CM1 and CM4 would often tread on a human hand, they never exhibited the final movements characteristic of cloacal contact nor the subsequent pPC display.

Throughout treading the captive males continued the pulses of the vWR begun during the pTW display. It was not ascertained whether the wild males also emitted this call during treading because of observation distances and the low intensity of the call.

Postcopulatory Display (pPC)

This display immediately followed the male's dismount and was given by both sexes. In the display the male circled or partially circled the female, who remained on the copulation site and turned her body to face the male as he circled. Captive males similarly circled the human following treading on the human hand. The male's tail was dropped (sector F or G), slightly fanned, and turned inward toward the female, while his head pointed upward (sector A or B) (Fig. 15a). At regular intervals in the circling he stopped, presenting a side view to the female, bowed his head (sector B or C), produced the vICO accompanied by a conspicuous throat bulge (Fig. 15b), then rapidly flicked his tail and head upward (tail to sector B-E, head to sector A-B) (Fig. 15c). He then either repeated this sequence, remaining stationary, or continued to circle before again stopping and repeating the sequence. The female exhibited the same display either simultaneously (Fig. 15d) or alternating with the male's display. Fig. 16b-e depicts the relative spatial positions of the displaying pairs for the

Figure 15. Postcopulatory display (pPC) and flick-bow display (pFK-B).

a-c. Postcopulatory display by captive pair.

a. Male in foreground circles female.

b. Male bows and gives vICO.

c. Male gives upward head and tail flick.

d. Simultaneous flick by WM2 and WF2 (to right).

e-f. pFK-B of CM1.

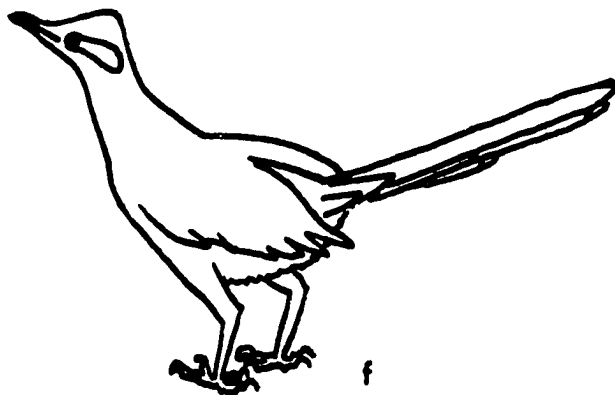
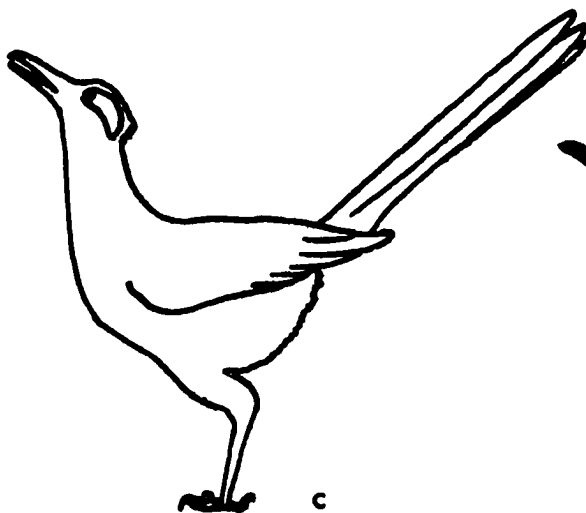
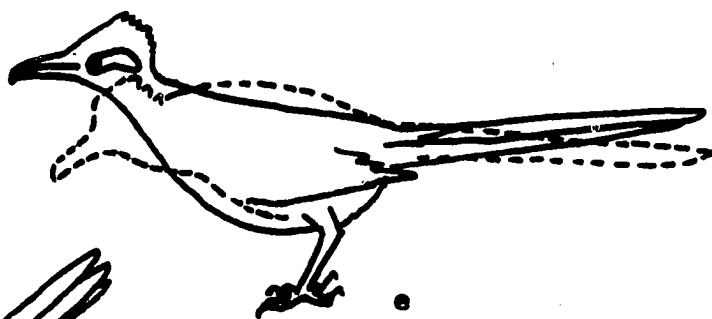
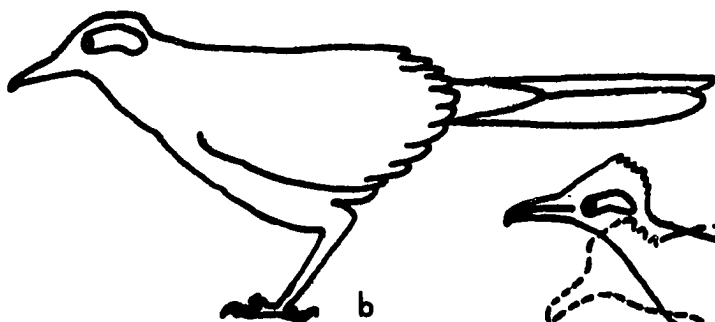
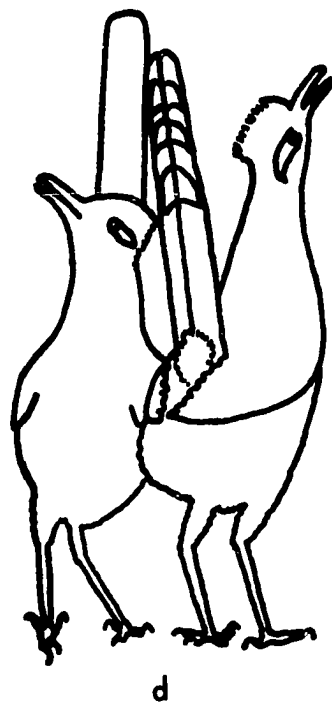
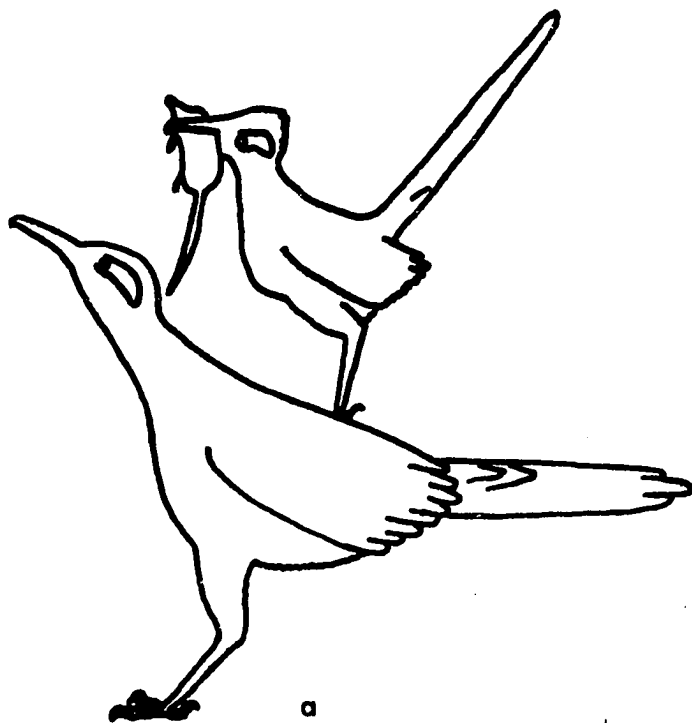
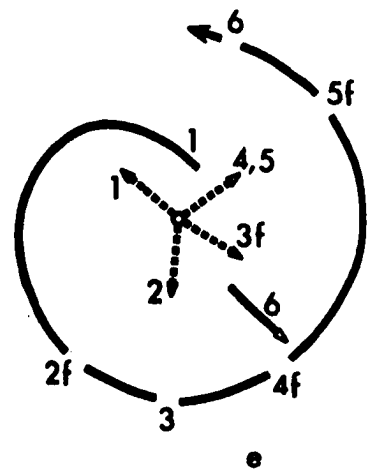
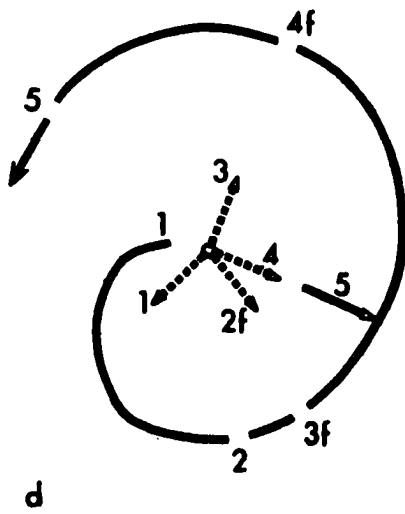
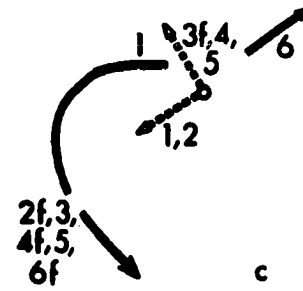
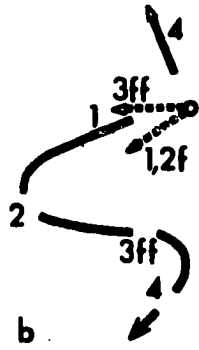
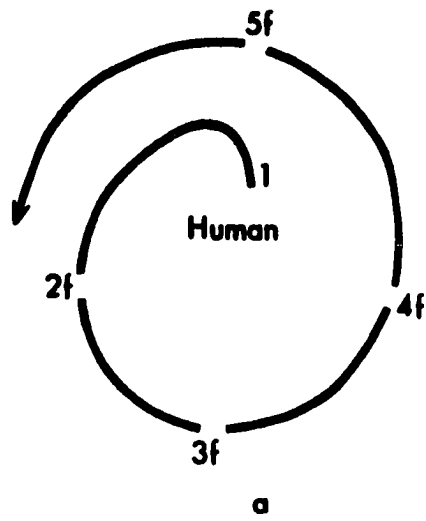


Figure 16. Top view of the postcopulatory display (pPC). Solid lines depict the male's pathway and dotted lines the female's position as she turns. The numbers indicate the male's and female's positions at the same point in time. "f" indicates the point where a click occurred; "ff" indicates that two flicks occurred at the same location. The arrows indicate the direction in which the female is facing and the solid arrow indicates the direction she takes as she leaves the area.

- a. CM3 performing the pPC to a human.
- b. pPC by wild pair 2.
- c. pPC by wild pair 2.
- d. pPC by the captive pair.
- e. pPC by the captive pair.



four separate episodes that were filmed, and Fig. 16a depicts the pathway of the CM3 as he displayed to a human.

The time-motion analysis of the display was divided into two time sequences: Phase 1 included the time when the head was highest in the flick until lowest in the bow, and Phase 2 represented the time when the head was lowest in the bow until highest in the flick. In addition, Phase 3 encompassed parts of both phases, including the time when the tail was first lowered after the flick until the head began bowing. The time for the entire cycle was measured from one high point of the head flick until the next. The pPC display had a definite time-motion pattern (Table 7), with Phase 1 averaging more than twice as long as Phase 2. Within a cycle, Phase 2 (range=.17-.94) was always shorter than Phase 1 (range=.66-2.22). The tail reached its maximum height in the flick slightly later (60-80 m sec) than did the head.

In all birds the wings were dropped below normal during the bow and lifted above normal with the flick (Fig. 15b, c). The crest was sleeked or relaxed to slightly fluffed at the start of the display, becoming fluffed or fully ruffled near the end. The post-orbital patch was fully exposed in all birds, with the exception of WF3 in which the area was partially obscured early in the display.

Movements Accompanying Acoustic Signals

The head movements accompanying the vCO were conspicuous and exhibited a definite temporal pattern. The initial motion was a lowering of the head from the normal horizontal position (Fig. 17a). The crest was ruffled and the post-orbital area exposed as the head was lowered.

Table 7. Temporal characteristics of the pPC display of wild pair 2 and captive pair 1.

Time expressed in seconds.

	Phase 1 ¹			Phase 2 ²			Phase 3 ³			Total cycle ⁴		
	M	F	Total	M	F	Total	M	F	Total	M	F	Total
Mean	1.25	1.03	1.10	.46	.36	.43	.96	.52	.78	1.81	1.29	1.62
SE	.15	.22	.14	.05	.05	.04	.15	.08	.12	.18	.19	.14
No. units analyzed	12	5	17	17	9	26	16	6	16	11	6	17
No. birds	2	2	4	2	2	4	2	2	4	2	2	4

¹Time from head at highest point of flick until at low point in bow.

²Time from head at lowest point in bow until at highest point of flick.

³Time from the point that the tail is first lowered until the head begins to bow.

⁴Time for one complete cycle, measured from one high point of the flick to the next.

In the earlier movements the head lowered with successive inward motions, while during the latter movements it was raised slightly (Fig. 17b-e). This may be detected by using the base line provided for reference. In the final movement the head was raised to the erect position (Fig. 17f), after which the crest was sometimes lowered before the next vCO was given, although the post-orbital area remained exposed. A note of the vCO was produced with each forward head motion, accompanied by a conspicuous throat bulge (Fig. 17b-e). Thus the number of forward head motions corresponded to the number of notes in a vCO and exhibited intra- and intermale variation.

The temporal pattern of the vCO movements corresponded with the temporal analysis of the vCO note durations (Tables 2 and 6). Duration measures of all middle notes and head motions were averaged to allow for different note numbers per bird. Each successive forward-inward head motion averaged longer than the preceding, as did each note. The head raising time was slightly longer than the time required for a corresponding note to be produced, as the head was held stationary in the forward position for an instant after the note was given and prior to the inward head motion.

Head movements similar to those of the vCO accompanied the vSCO (Fig. 18a-b). Each note was given as the head moved forward, with the duration of the note and the head motion increasing for each successive note (Tables 2 and 6). As for the vCO movement, the head was held in the forward position following the production of the note. During vSCO production the crest was fully ruffled and the post-orbital area exposed.

The vWH was always given with the bird in the sitting or crouching

Figure 17. Head movements of CM3 while producing a 6 note vCO.

Each drawing represents the production of one note.

The solid line depicts the head as it is drawn nearest the body just before the note begins and the dotted line represents the head's position at the end of the note. The head is in the erect position at the beginning and end of one vCO sequence.

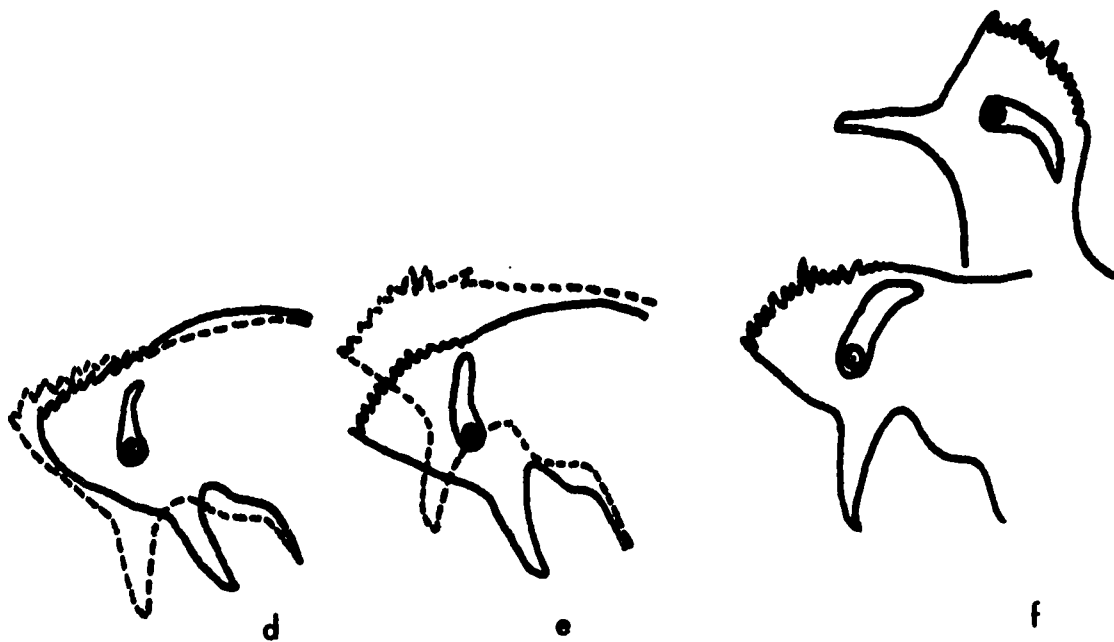
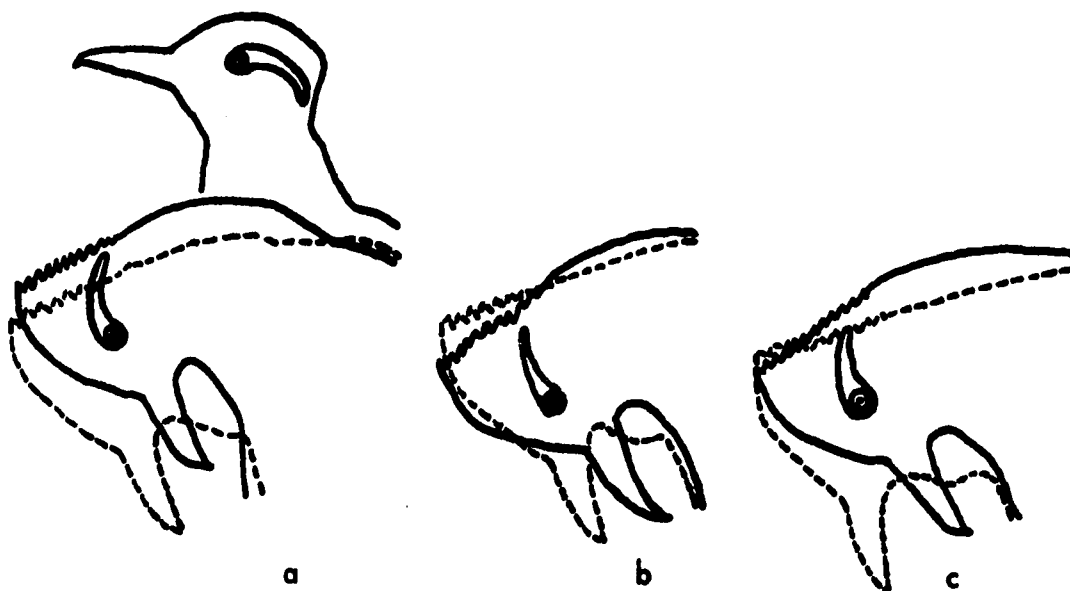
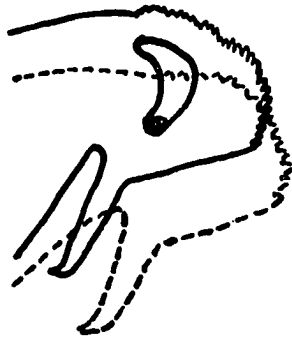
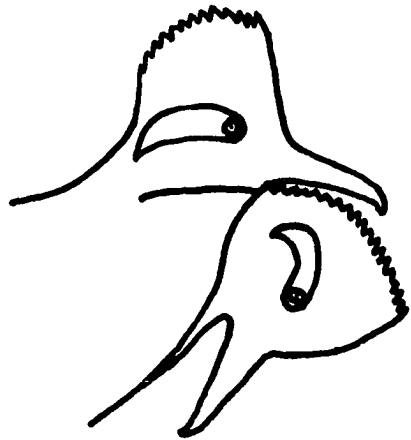


Figure 18. Body postures associated with various courtship acoustic signals.

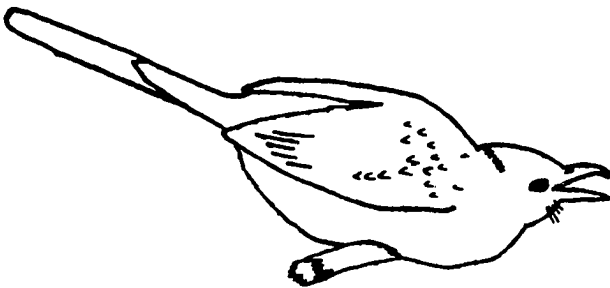
- a. vSCO of 2 notes by WM5. The solid line represents the head just prior to the beginning of the first note; the dotted line represents the head position at the end of the first note.**
- b. The last note of the vSCO of WM5.**
- c. Posture during vWH by CF1.**
- d. Posture of fledgling as it begs from WM3 (to left).**



a



b



c



d

position (Fig. 18c). The basic movement was a vertical displacement of the head from sectors B to E or F. During the downward movement from 3-6 horizontal head shakes were given. These shakes appeared to be involuntary or convulsive in nature. Initially, the bill was held open at an angle of 50-60 degrees as the WH signal was being produced, but gradually closed as the head reached the lowest point of the vertical movement. Thus one vertical displacement corresponded to one vWH note. The feathers and crest were sleeked during this time and the post-orbital area was obscured. The eyes would close briefly at times. The begging posture of a fledgling roadrunner is presented (Fig. 18d) for comparison with that of the vWH position.

For each note of the vGC signal the throat bulged conspicuously. The bird stood with feathers slightly fluffed, with crest ruffled or fully ruffled, and the post-orbital area partially obscured.

No significant movements accompanied the vCK except for the bill snapping which produced the noise portion of the signal. The bird stood erectly with crest fluffed or ruffled and post-orbital area in various stages of exposure.

During the vBR the bird's body was seen to jerk slightly with each note and the bill was opened only slightly. Crest posture varied from normal to fluffed, and the post-orbital area exhibited various stages of exposure.

Postures accompanying the remaining acoustic signals, vPOP, vWR, and vICO, were discussed earlier in this chapter.

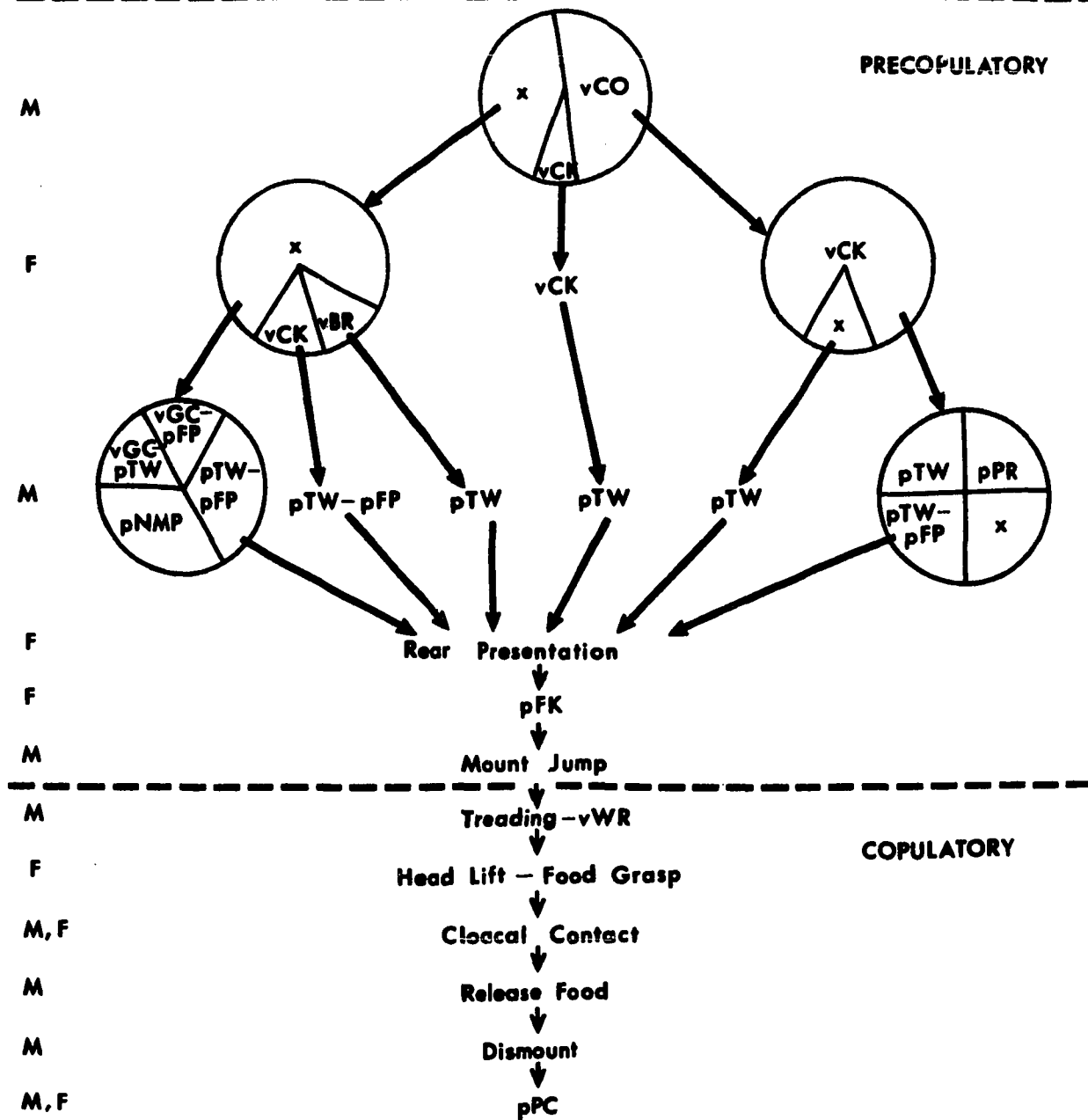
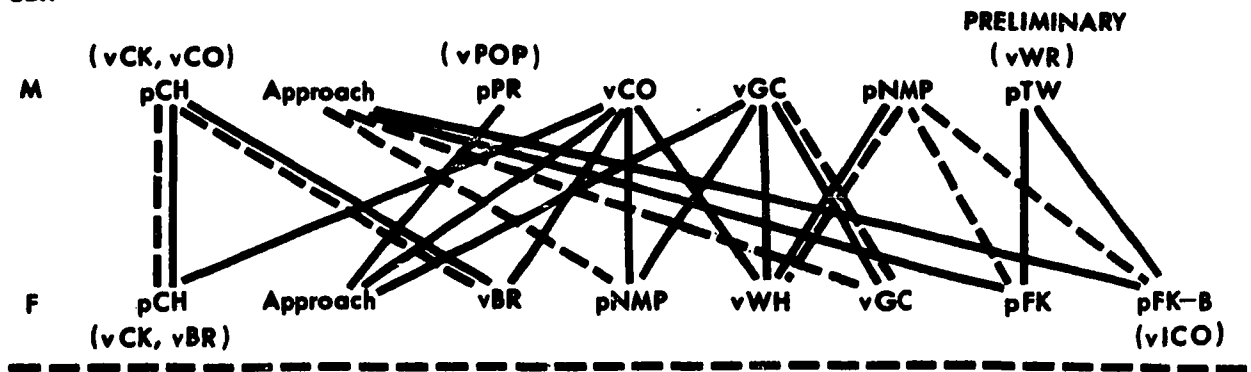
Summary of Courtship and Copulatory Patterns

The characteristic preliminary, precopulatory, and copulatory be-

havior patterns of the roadrunner are summarized in Fig. 19. The most frequent interactions between the sexes during the preliminary phases are indicated in the figure with the solid line representing male-initiated sequences and the dotted line representing female-initiated sequences. The symbols in parenthesis indicate the vocalizations that accompanied the posture. The precopulatory and copulatory sequences presented in the figure are based on observations of thirteen successful copulations of wild pairs. The variation that was exhibited by these pairs in the precopulatory phase is presented as sectors of a circle, representing per cent of occurrence of the behavior. The copulatory behavior pattern of these pairs did not vary.

Figure 19. Summary of roadrunner courtship and copulatory patterns.

M=male, F=female. In the preliminary phase the dotted line indicates a female-initiated sequence and the solid line indicates a male-initiated sequence. In the pre-copulatory phase the sectors represent per cent occurrence. The "x" indicates that no observable behavior occurred.

SEX

CHAPTER VII

COURTSHIP PATTERNS AND THE BREEDING CYCLE

Introduction and Methods

As is typical of many avian species, the roadrunner pair remains together throughout the breeding cycle, in contrast to other avian species in which the pair comes together only briefly for courtship and copulation. In the latter case only one sex assumes all parental duties (Lack, 1940b). For the former group there is a possibility that courtship behavior continues during nesting, but its form may change as the breeding cycle progresses. This aspect is infrequently considered in avian courtship studies, and hence the description of a courtship pattern based on observations during only one breeding phase may not necessarily be characteristic of another phase.

In this study observations were made on pairs throughout their breeding cycle, obtaining quantitative and qualitative data on courtship pattern changes. To aid in analysis, the breeding cycle was divided into six phases. These divisions were logical for the roadrunner's breeding cycle, but may not apply to that of other avian species. The phases are delineated below with the symbol to be used for each.

Pair Formation-BP1

Pair formation was the most difficult phase to determine and to

recognize in the field as there were no definite objects such as nests or eggs to serve as objective criteria. Birds were considered to be in this phase only early in the breeding season (February and early March). Only preliminary aspects of courtship, but no copulatory or nest building behaviors were exhibited. Breeding pairs 4, 8, 12, and 13 and WU 2, 3, 4, 5, and 6 were observed for a total of 43 hours in this phase.

Pre-Egg-Laying Phase-BP2

In this phase nest site selection and nest construction occurred, but no eggs were yet laid. Wild pairs 2, 3, and 9 were observed for 28 hours in this phase.

Egg-Laying-Incubation Phase-BP3

This phase began when the first egg was laid and continued until the time of its hatching. The roadrunner begins incubation when the first egg is laid, resulting in staggered hatching dates. Wild pairs 2, 3, and 11 were observed in this phase for 152 hours.

Nestling Care I-BP4

This phase extended from the time the first egg hatched until the first nestling was 12-13 days old. During this phase at least one parent was always present at the nest, with the nestlings being brooded almost continuously. Wild pairs 2, 3, 6, 7, 10, and 11 were observed for a total of 165 hours in this phase.

Nestling Care 2-BP5

This phase extended from the end of BP4 until the majority of the nestlings had fledged, usually at 19-20 days of age. Brooding during

the day and feeding rates decreased during this phase, and both parents were absent from the nesting area for long periods. Wild pairs 2, 4, 6, 7, and 10 were observed for 100 hours during this phase.

Fledgling Care-BP6

This phase extended from the time the young fledged until they fed independently, between 30-40 days later. Wild pairs 1, 2, and 6 were observed for 103 hours during this phase.

Breeding Cycles of Captive Birds

Breeding cycle distortions were exhibited by the captive pair, perhaps due to the effects of hand-rearing, to inappropriate environmental situations, or to both. Nest-building, accomplished in a few days by wild pairs, extended over 26 days in captivity. Incubation was intermittent with no eggs hatching, and many additional attempts at nest construction occurred during the incubation period. Thus, in captivity only the first three breeding phases were observed.

As CM2, 3, and 4 did not have mates, all courtship exhibited by them was considered to represent BP1 and 2. CM2 and CM3 were released at site A, and CM4 was released at site E during the breeding season and their behaviors observed. CM2 and CM3 encountered wild birds in BP1, and CM2 also interacted with wild birds in BP6.

Results

The courtship behaviors and their occurrence during each breeding phase are presented in Table 8 for wild pairs and Table 9 for the captive pair. To equalize the disparate observation periods, the frequencies (Table 6) were adjusted, using BP4 values as a base line, in order

Table 8. Occurrence¹ of the various courtship behaviors of wild roadrunners during each breeding phase.

Behavior	Breeding Phase					
	1	2	3	4	5	6
pCH	7.6 ²	3.4 ^{mf}				8.0 ^{mf}
vCK	38.4	70.8 ^{mf}	27.0 ^{mf}	49.0 ^{mf}	37.9 ^{mf}	65.6 ^{mf}
vCO	65.3	47.2 ^m	6.5 ^m	5.0 ^m	4.9 ^m	19.9 ^m
vBR	30.7	76.6 ^{mf}	20.5 ^f	4.0 ^f	18.1 ^{mf}	30.4 ^{mf}
vGC	11.5	44.8 ^{mf}	7.6 ^m	4.0 ^m	4.9 ^m	17.6 ^m
vWH	23.0	35.4 ^f	3.2 ^f	1.0 ^f	1.6 ^f	3.2 ^{mf}
pTW	6.8	11.8 ^m	6.6 ^m	2.0 ^m		9.6 ^m
pFK	3.2	5.9 ^f	12.3 ^f	2.0 ^f	1.6 ^f	10.9 ^f
pFK-B	1.5	5.9 ^f	1.1 ^f	1.0 ^f		1.6 ^f
pNMP	4.2	23.6 ^{mf}	1.1 ^m		1.6 ^f	6.4 ^{mf}
pFP		5.9 ^m	4.4 ^m	2.0 ^m	1.6 ^m	1.6 ^m
pPR			1.1 ^m		1.6 ^m	
vGCO				15.0 ^{mf}	26.4 ^{mf}	33.6 ^{mf}
CP-S ³		5.9	5.5	1.0	1.6	1.6
CP-U ⁴			4.4	1.0		8.0

¹Values adjusted to account for unequal observation times

²Sex unknown in this column

^mKnown males performed the behavior

^fKnown females performed the behavior

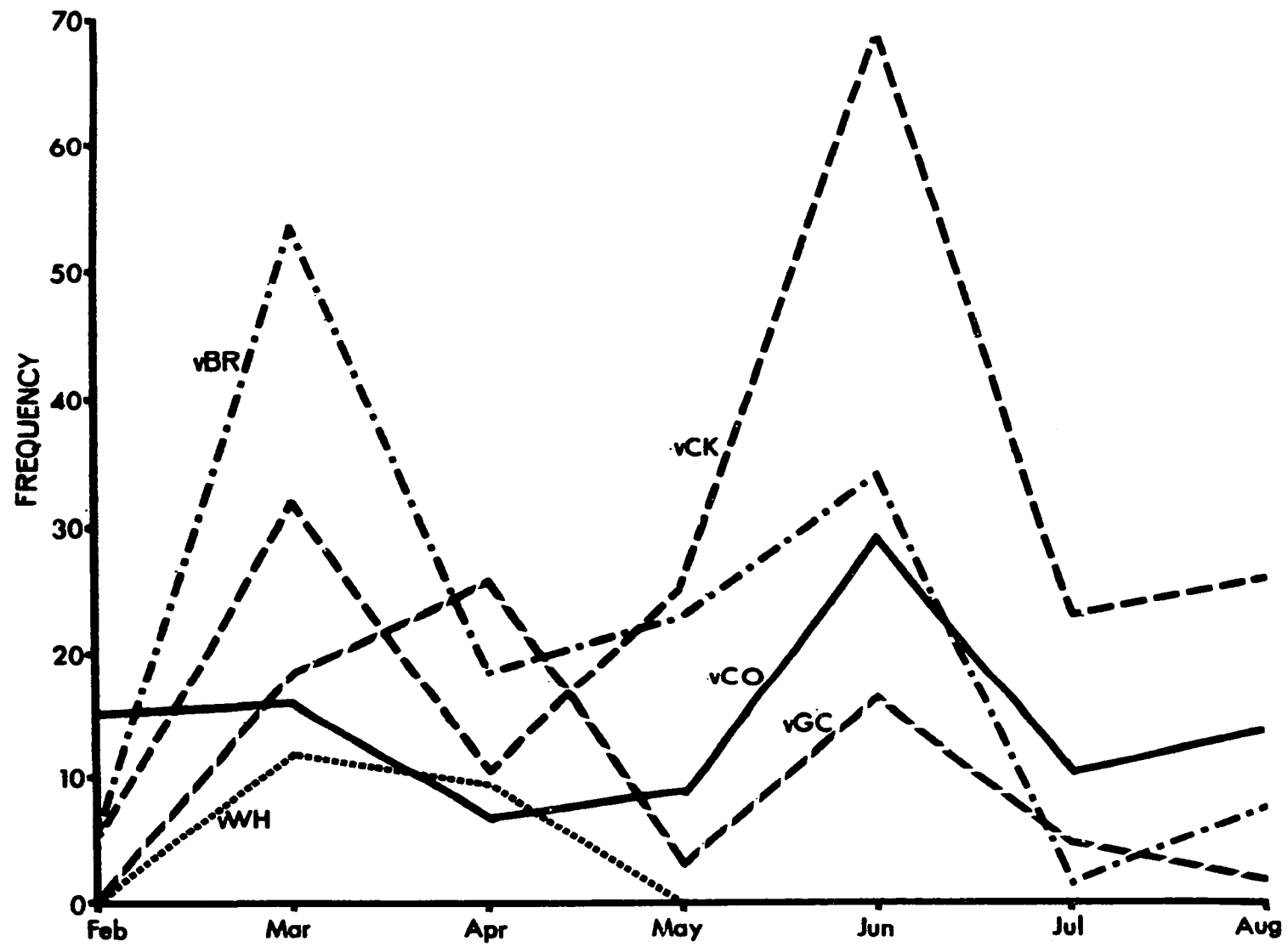
³Successful copulations

⁴Unsuccessful copulations

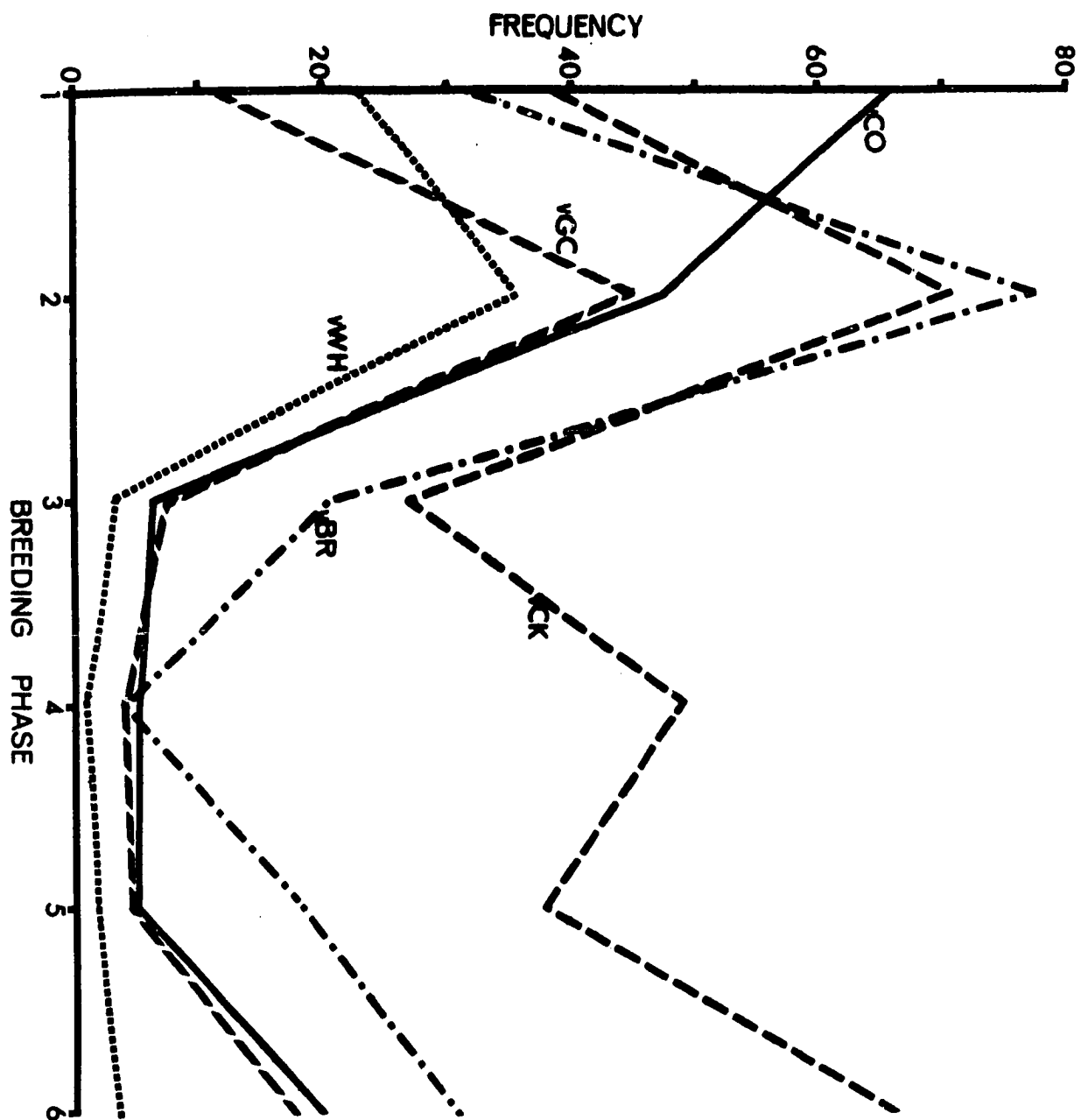
Table 9. Occurrence of the various courtship behaviors during each breeding phase of the captive breeding pair during their first breeding season (1969).

Behavior	BP1		BP2		BP3	
	M	F	M	F	M	F
vCO	35		15		2	
vSCO	4		3		2	
vCK	7	15	5	15	1	2
vGC	8	3	14	10	20	18
vWH	11	6	14	14	10	5
vBR		10		22		3
pFK	7	20	9	7	3	12
pFK-B		1		11		5
pNMP	10	15	10	6	1	
pPR	12				10	
pTW	35		54		40	
pCH		13	17	5		1
CP-S			7		8	
CP-U	1		9			
Length of phase	61 days		26 days		20 days	
Hours observation	54		48		25	

Figure 20. Occurrence of the courtship acoustic signals throughout the breeding season at Big Bend National Park and South Texas sites.



**Figure 21. Occurrence of courtship acoustic signals throughout the breeding cycle
at all sites.**



that comparisons between the phases could readily be made. In Table 9 the values were not adjusted as the observational hours were not as disparate as for those on wild birds. These tables denote which sex performed the behavior and also indicate the number of successful and unsuccessful copulations observed for each phase. Unsuccessful copulations were those in which the male attempted to mount, but was not allowed to do so by the female, or when she displaced him after only a few seconds of treading. A successful copulation was consistently followed by the pPC display.

As acoustic behavior was prominent in roadrunner courtship, the occurrence of the major acoustic signals for each month of the breeding season were graphed in Fig. 20, while the occurrence of these same signals for each breeding phase are presented in Fig. 21. Only the South Texas and Big Bend National Park sites were included in the seasonal data to avoid compounding data with the more northern Oklahoma latitudes. The data in Fig. 20 were adjusted to account for different observational periods per month.

Table 8 indicates that courtship was displayed by wild pairs throughout the breeding cycle, with qualitative, quantitative, and sexual variation of the courtship pattern in different phases. Courtship culminated in copulation in BP2-6, despite the fact that after BP3 egg fertilization was no longer necessary. Preliminary courtship behaviors were most frequent in BP1, 2, and 6. Precopulatory behaviors were most frequent in BP2, 3, and 6, and reduced in BP4 and 5.

During BP1 the pair would forage together daily, but keeping several m apart, and often would be separated for long periods during the day. The pair was observed roosting together in the same shrub or

tree occasionally. Only preliminary courtship occurred during this phase, with acoustic signals being very prominent. The vCO, vBR, and vCK signals were most often given when the bird was alone. While giving the vCO, the bird was always observed to be in an elevated, exposed position, such as at the top of a dead tree. It was most often emitted in the early morning, at several minute intervals, for periods from 30 minutes to several hours without the bird changing location. The vBR was heard equally throughout the day, with the bird in various locations while calling. Usually only a few sequences were emitted at one time. Observations on the vCK were similar to those of the vBR. These three signals were also incorporated into the pCH (Chapter V). The vGC and vWH were always given when another bird was near, either during the pCH or as the birds foraged together, as were pNMP and pTW.

Mutual pTW displays were observed on several occasions during BP1, suggesting that during pair formation the female may also exhibit pTW. However, as the sexes could not be identified during this phase, these could have been male-male encounters. Another suggestion that perhaps the female exhibited the pTW was that on several occasions a wild roadrunner at site A performed the pTW in front of CM2.

Several wild birds in BP1 at site A exhibited pCH and vBR behaviors toward CM3 after his release at site A.

During BP2 preliminary, precopulatory, and copulatory behaviors were exhibited in their highest frequencies of the entire cycle. The vCO was an exception, however, being lower in frequency than in BP1. The vCO was given both when the male was separated from the female and as a precopulatory signal. Many of the vBRs were given by the female as she foraged near her male in response to distant vBRs. The male

exhibited no observable response to the vBRs. The vGC was given more frequently by the male, although occasional mutual calling would occur as the pair foraged together. Nearly all pNMP occurred during this phase, was most often exhibited by the female, and was prior to nest building. Copulation was observed along with behavior suggesting nest site selection (frequent trips up into trees and shrubs by the pair). Wild pair 3 was observed in successful copulation at the site of their future nest. The vWH of the female was always given from a tree or shrub near the male. However, most vWH signals were given by the female from or near the partially completed nest. The pFK and pFK-B were given by the female as approached by the male. Preceding copulation on various occasions were pTW, pFP, or pNMP by the male and pFK by the female.

During BP3 the same diversity of behaviors was exhibited as during the previous phase, although less frequently. The vCK and vBR were the most frequent acoustic signals, and the majority of both signals were given as the bird was on or near the nest. Many of the vBRs were given by the incubating female in response to distant vBRs. The vCKs were often mutually given between the incubating bird and its nearby mate. The vGC was given by the male as he foraged near the nest. The male's vCO was given as he approached the nest and usually preceded copulation or attempts to mount. Copulation was only slightly less frequent than in BP2 and always occurred at the nest site. On every occasion observed the male gave the vCO or vCK as he approached the nest, but while still out of sight, and began the pTW as he reached the nest tree. The female on the nest either gave the vCK or was silent a moment before leaving. Copulation then occurred, usually within 5 m of the nest.

pNMP occurred only rarely and was exhibited only by the male. Both sexes continued to add lining material to the nest during this phase.

During BP4 the vCK was by far the most frequent acoustic signal, and was given in the same situations described for BP3. All other acoustic signals, pNMP, and copulation dropped to their lowest occurrences.

During BP5 copulation occasionally occurred, but was not preceded by the male's precopulatory displays other than pFP. The pFK of the female was consistently given, however. Acoustic signals increased in frequency with the exception of the vCO. pNMP was exhibited by WF2, who was simultaneously engaged in construction of a second nest 20 m from the first one.

During BP6 there was a resurgence of courtship behavior, correlated with simultaneous reneating in wild pair 2 and possible subsequent reneating in the other pairs. Not only precopulatory but also preliminary behaviors gained prominence although not reaching the frequencies exhibited in BP2. Even though pTW increased during BP6, pFP did not, the male in these cases approaching the female with no food. Also, the highest frequency of unsuccessful copulations occurred during this time. The majority of the unsuccessful copulations were observed in wild pair 1, a pair that possibly did not reneate. The majority of the vBRs were given by the male in response to distant vBRs or upon the appearance of a strange roadrunner in the area, often followed by attack and chase of the stranger. These encounters usually occurred as a male accompanied fledglings. The sexual pCH seen during this phase, in contrast to that of BP1 and BP2, usually included several attempted copulations. The vWH of the female was given during

nest building, and also once by WM2 as he carried sticks to the second nest.

Several behaviors presented in Table 8, although occurring during the breeding season, were not integrated into courtship patterns. The vGCO of BP4, 5, and 6 was identical in physical characteristics to the vGC, but was given to nestlings and fledglings in association with feeding, leaving the nest, and location after fledging. The pPR behavior of the male occurred in BP3 and 5 only, and was exhibited by the male as he ran away from the nest where the female was incubating or brooding.

Comparing the frequency pattern of acoustic signals during the breeding cycle with that occurring during the breeding season, similar trends are seen (Fig. 20, 21). All acoustic signals were frequent both early in the cycle and in the season, decreasing in frequency in BP 3-5 and in April-May. A resurgence of signals occurred in BP6 and in June.

During the breeding phases of the captive pair, courtship patterns similar to those exhibited during the wild breeding phases were observed. Acoustic signals were more prominent during BP1, with the exception of the vGC, which increased during BP3. It should be noted, however, that the majority of the vGC during BP3 were given by both sexes during a short period when the female was eggbound, a situation not observed in the wild. Although the vSCO was never given by the wild male in association with pair behavior, CM1 exhibited this signal simultaneously with pTW and pFP both to CF1 and to humans. The vWH was given by CM1 much more frequently than by wild males, while the pFK-B was exhibited more frequently by the captive female than by any of the wild females. In BP1 the female was the aggressor in the pCH, while

in BP2 the male was more often the aggressor, and the behavior almost disappeared in BP3. The pPR of CM1 appeared in BP3 only when the pair bond had apparently broken, following a cessation of incubation and preceding a new nest building attempt. Its high frequency correlated with increased pTW displays to humans, and it was most often given when a human appeared suddenly near the enclosure.

The captive males without mates exhibited variation in their courtship pattern throughout the season, also. Earliest in the season were vCQ and pNMP, preceding any precopulatory behavior by several weeks. Chasing of one another also occurred during this time. In addition, CM3 exhibited aggressive behavior toward humans, chasing and attacking often. Later in the season these aggressive displays alternated with courtship behaviors, especially with pTW. The pTW preceded any attempts to mount the human hand by several days, while the cloacal contact motions and pPC display were not exhibited until even later. Neither CM2 nor CM3 exhibited the pPR display during their first breeding season. However, during his release into the wild at site A in his second breeding season, CM3 exhibited the display to humans. CM4 exhibited pPR in captivity and after release at site E to humans. Although no nest building was observed in captivity, CM2 and CM4 built nests after release into the wild.

CHAPTER VIII

ACOUSTIC COMMUNICATION PATTERNS

Introduction and Methods

During this study the prominence of acoustic signals in the courtship of the roadrunner became apparent. This aspect of the research was to investigate more thoroughly the communicative value of these acoustic signals.

By observing the context and response pattern to a given acoustic signal, it is possible to gain an understanding of its communicative value (Marler, 1956a). Throughout the field investigations, notes were kept on the context of each acoustic signal and acoustic responses to that signal. A response was arbitrarily defined as acoustic behavior that followed the initial signal within one minute. Quantitative data were obtained on all wild birds during the breeding season, while only qualitative data were obtained on the captive birds. It was hypothesized that if a signal had communicative value, responses to that signal would not be random. The 2-cell chi-square test using Yate's correction factor for small samples was applied to the data to determine significant signal-response associations. The expected values for the test were based on the assumption that occurrences of a particular response would be equal after each initial signal.

Results

Acoustic responses of roadrunners to an initial acoustic signal are presented in Table 10. The table also includes observations on situations where no response was given. The frequencies presented are the totals for wild birds, while the superscripts indicate the patterns given by both wild and captive breeding pairs. Also indicated are those patterns which immediately preceded copulation in the wild pairs.

Certain acoustic patterns were found to occur more frequently than were others. Patterns found to be significantly more frequent by the chi-square test (.01, $p=6.63$) were: vCO-vCO, vCO-vWH, vBR-vBR, vCK-vCK. Other patterns, slightly less significant (.05, $p=3.84$), were vGC-vWH and vGC-vGC. Several patterns were exhibited only by the captive pair (vWH-vBR, vWH-vCK, vWH-vWH), while others were exhibited by the captive pair and unpaired wild birds, but not by the wild pairs (vBR-vCO, vCO-vBR). Four patterns recorded for wild paired and unpaired birds were not exhibited in captivity (vCK-vBR, vGC-vBR, vGC-vWH, vWH-vGC). The significant acoustic patterns of wild birds and their contexts are discussed below.

vCO-vCO

This pattern was always given by birds that were widely spaced (at least 50 m apart). It was heard primarily in the early morning, often for periods of two hours or more, with the birds alternating their calls, and usually remaining in the same location for the duration of the calling period. This pattern was seldom exhibited by a member of a wild breeding pair.

vBR-vBR

This pattern was also given by widely spaced birds, although not for the long periods reported above. It was never exchanged between paired birds, but was often given by the paired female, especially during BP2 as she foraged with the male or during BP3 while incubating. WM2 participated in this pattern during BP6 when accompanying fledglings.

vCK-vCK

This was the most common communication exhibited in the wild, and also between members of a wild pair. It was heard in a variety of situations throughout the breeding season: BP1 during the vCH; BP1, 2 as the pair foraged together; BP3, 4, 5 as one pair member was on the nest and the other approached the nest or foraged nearby; BP6 as a parent accompanied the fledglings while the other was foraging nearby. On several occasions this response pattern preceded copulation.

vCO-vWH

This pattern was exhibited by both captive and wild pairs, primarily during BP2 in association with preliminary courtship. The pair was usually separated (20-40 m), and each was in an elevated position, as is characteristic for both signals.

vGC-vWH

This male-female pattern was heard during BP1 and 2 as part of preliminary courtship. Usually the sequence was given when the birds were in close proximity.

Table 10. Occurrence of acoustic communication patterns of wild roadrunners during the breeding season. A response was defined as one following the initial signal within one minute.

Initial Signal	Response						
	vCO	vBR	vCK	vGC	vWH	0 ¹	0 ²
vCO	8	5 ^c	9 ^{wc+}	2 ^w	8 ^{wc}	21 ^{wc+}	47 ^{wc}
vBR	2 ^c	18	10	2 ^{wc}	2	39 ^{wc+}	35
vCK		2 ^w	36 ^{wc+}			47 ^{wc+}	71
vGC		1 ^w	2 ^{wc+}	6 ^{wc}	4 ^w	17 ^{wc+}	2
vWH		c	c	1 ^w	c	8 ^{wc}	

¹Situations when another roadrunner was in sight when the initial signal was given, but did not respond.

²Situations when no other roadrunner was in sight when the initial signal was given, and no response occurred.

^wOccurrence in wild breeding pairs.

^cOccurrence in captive breeding pair.

⁺Immediately preceded a copulation in the wild pairs.

vGC-vGC

The vGC was often exchanged between paired birds in the wild and in captivity. Early in pair formation it was common as the pair foraged together. Later it was less frequently given, but did occur in the nesting area.

vCO-vCK

Although not statistically significant, this pattern is included as it was the most common one preceding copulation. Most frequently the male would give the vCO at some distance from the female (20-50 m), and she would respond with the vCK as the male approached, usually exhibiting the pTW.

Signals by Solitary Individuals

The vCO, vBR, and vCK were the most frequent signals given when no other bird was in sight, and with no reciprocating responses (Table 10). After several repetitions of the signal with no response, the vBR and vCK would be terminated, although the vCO would be repeated for long periods. The vCK signal by a solitary bird was usually exhibited as the bird encountered a strange object in the environment or just prior to or following a change in position or location. In contrast to the above signals, the vWH and vGC were rarely given when another bird was not nearby.

Signals by Captive Unpaired Males

CM2, and 3 exhibited the vCO signal often during the breeding season, although the alternating vCO-vCO pattern was never heard. When released into the wild, however, CM2 exhibited the vCO in response to

distant vCOs on many occasions. The most common response pattern between CM2 and 3 during the breeding season was the vCK-vCK. The only other pattern exhibited was the vCO-vGC between CM3 and CU1.

CHAPTER IX

RESPONSE-ELICITING PROPERTIES OF THE vCO

Introduction and Methods

As the vCO was a prominent initial signal in breeding season communication patterns and frequently preceded copulation, further study of its communicative value was warranted. This aspect of the research was conducted on the response-eliciting properties of the vCO for wild and captive birds.

The method employed was to present the vCO alone to a wild or captive bird, thus eliminating all visual cues normally present when the vCO was given by a roadrunner. The test signal used was either a previously recorded vCO of a wild male played back on the Uher tape recorder or an artificial sound (ART-vCO) with physical properties similar to those of the vCO (Tables 1 and 3). The test signal was presented from a car parked near the roadrunner or in areas where roadrunners were known to occur frequently. The signal was presented to the wild breeding pairs in their breeding territory. The signal was presented every minute until a bird appeared or, if a bird were already present, until a response was exhibited. The rate of presentation was then decreased to every 3-4 minutes. To test captive birds the signal was presented at distances of 10-15 m from the enclosure, usually from a parked car.

The test signal was presented to 230 wild birds during the 1967, 1968, and 1969 breeding seasons at all study sites. All behaviors immediately preceding and following the presentation of the test signal were noted, and several of the acoustic responses were tape-recorded.

The vCO and ART-vCO were also presented to captive and wild birds during the non-breeding season and responses noted.

Preliminary research on the response-eliciting properties of the vBR was also conducted for captive birds and are reported in this chapter. A recorded vBR of a wild female was presented to the captive breeding pair during their first breeding season (1969) and their responses noted.

Results

The test signal elicited a variety of male and female courtship behaviors. No differences in response to the vCO or the ART-vCO were noted. Responses to the vCO or ART-vCO are presented as percentages in Fig. 22 for all wild birds tested, including the wild pairs. There were two initial response types: birds that left the area immediately (17%) and those that approached the sound source (83%). Often the roadrunner would approach to within only a few m of the sound source. Of the approaching birds, some gave the vCO in response (58%), while others did not exhibit the vCO (42%). The remaining responses which were exhibited were grouped according to their association with the presence or absence of the vCO response for the individual (Fig. 22). The most frequent response exhibited by those not giving the vCO response was the vBR. The association of other courtship responses

Figure 22. Responses of wild roadrunners to the vCO playback. Numbers indicate percentage of the total for each level.

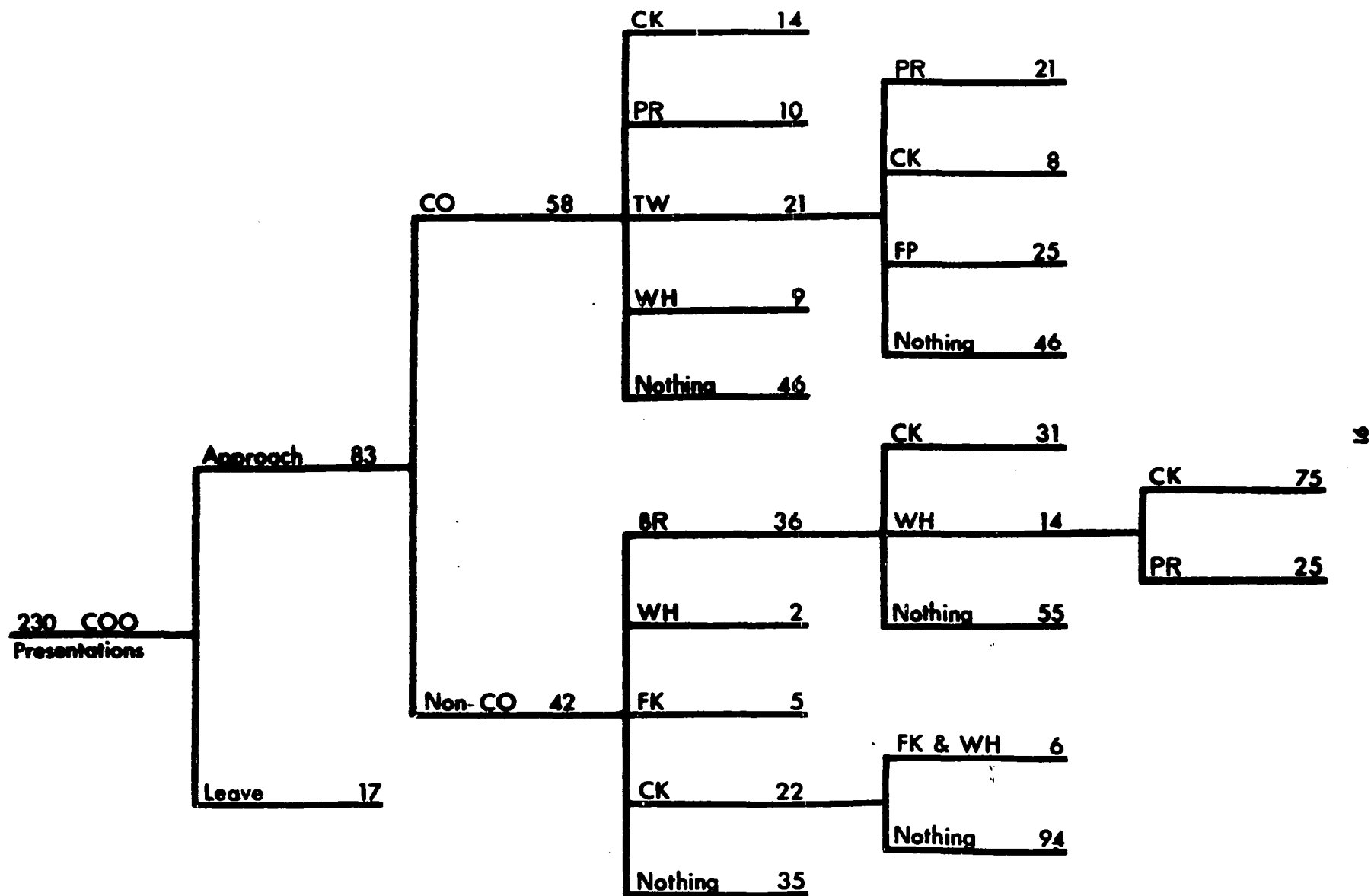


Table 11. Association of the various courtship behaviors with the vCO or vBR during the vCO playback experiment. Values represent number of occurrences.

Associated Behavior	Response		
	vCO	vBR	Neither
pTW	24		
pPR	16	1	
vCK	18	12	18
vWH	1	4	3
pFP	6		
pFK			5
No. responding	110	29	52

with either the vCO or the vBR response is presented in Table 11. The greatest variety of courtship behaviors were exhibited by the birds that gave the vCO response.

The responses of the wild breeding pairs to the test signal during the various breeding phases are presented in Table 12, along with the sex exhibiting each response. Most noticeable is the diversity of responses exhibited by both sexes during BP2, including both preliminary and precopulatory courtship behaviors. The males exhibited frequent responses throughout the cycle, whereas the females rarely or never responded during BP3, 4, or 5. The pPN response, not previously described, was a rapid breast or flank preening (Fig. 25d).

Responses to the test signal for each month of the breeding season for Big Bend and South Texas sites are presented in Table 13. The Oklahoma sites were again omitted to avoid seasonal variation. Unlike the pattern of breeding pair responses, a relatively constant level of response diversity was exhibited throughout the season.

As the acoustic signals were of special interest in this research, their occurrences in response to the test signal were graphed in Fig. 23 and Fig. 24. It is evident that the acoustic response pattern during one breeding cycle is similar to that exhibited throughout the breeding season. Comparing the responses to the vCO (Fig. 22) with naturally occurring acoustic behavior (Fig. 21) for each breeding phase, it is seen that the vBR and vWH signals, primarily female signals, exhibited similar trends of low frequency during BP3-5 in each situation. On the other hand, the vCO of the male exhibited very different frequencies in each situation, being

Table 12. Responses of wild roadrunners to the vCO playback during each breeding phase. Values represent per cent of the tests in which that response was given.

Response	Breeding Phase					
	1	2	3	4	5	6
Approach ¹	12.1*	33.3 ^{mf}				16.7 ^{mf}
pCH	9.1	4.7 ^m				
pNMP		4.7 ^f				
vWH	15.1	14.2 ^f				
pFK			16.7 ^f			
vBR	36.3	28.5 ^f				8.3 ^{mf}
pPN		4.7 ^f	16.2 ^m		18.1 ^{mf}	
pPR	12.1	4.7 ^m	33.3 ^m	11.1 ^m	45.4 ^m	29.1 ^{mf}
vCK	15.1	23.8 ^{mf}	16.7 ^m	11.1 ^m	45.4 ^m	29.1 ^{mf}
vCO	21.2	42.8 ^m	50.0 ^m	66.7 ^m	90.9 ^m	83.3 ^m
pTW		4.7 ^m	33.3 ^m	11.1 ^m	36.2 ^m	12.5 ^m
pFP					9.1 ^m	4.1 ^m
No. tests	33	21	6	9	11	24
No. birds tested	31	10	6	8	8	6

¹ Approached the sound source only and gave no further response.

* Sexes not determined for this row.

^m Males exhibited the response.

^f Females exhibited the response.

Table 13. Responses of wild roadrunners to the vCO playback during each month of the breeding season at the South Texas and Big Bend National Park sites. Values represent per cent of birds tested that responded.

Behavior	Feb	Mar	Apr	May	Jun	Jul	Aug
Approach*	91.6	71.4	50.0	83.3	90.3	85.7	90.0
vBR	25.0	23.8		11.1	8.0	17.9	5.0
vCO	25.0	23.8	31.8	55.5	54.8	59.0	60.0
pTW		2.3	4.5	19.4	8.0	13.6	36.3
pPR	25.0	4.7	13.6	8.3	4.8	3.6	9.0
vCK	33.3	26.1	4.5	22.2	9.6	46.4	72.7
pPN		2.3		11.1	1.6		
vWH		9.5					18.1
pFP			4.5	5.5	6.4		9.0
pFK			4.5	2.2			
No. birds tested	12	42	22	36	62	28	20

*Includes all those that approached the sound source.

Figure 23. Acoustic responses of paired wild roadrunners to the vCO playback throughout the breeding cycle at all sites.

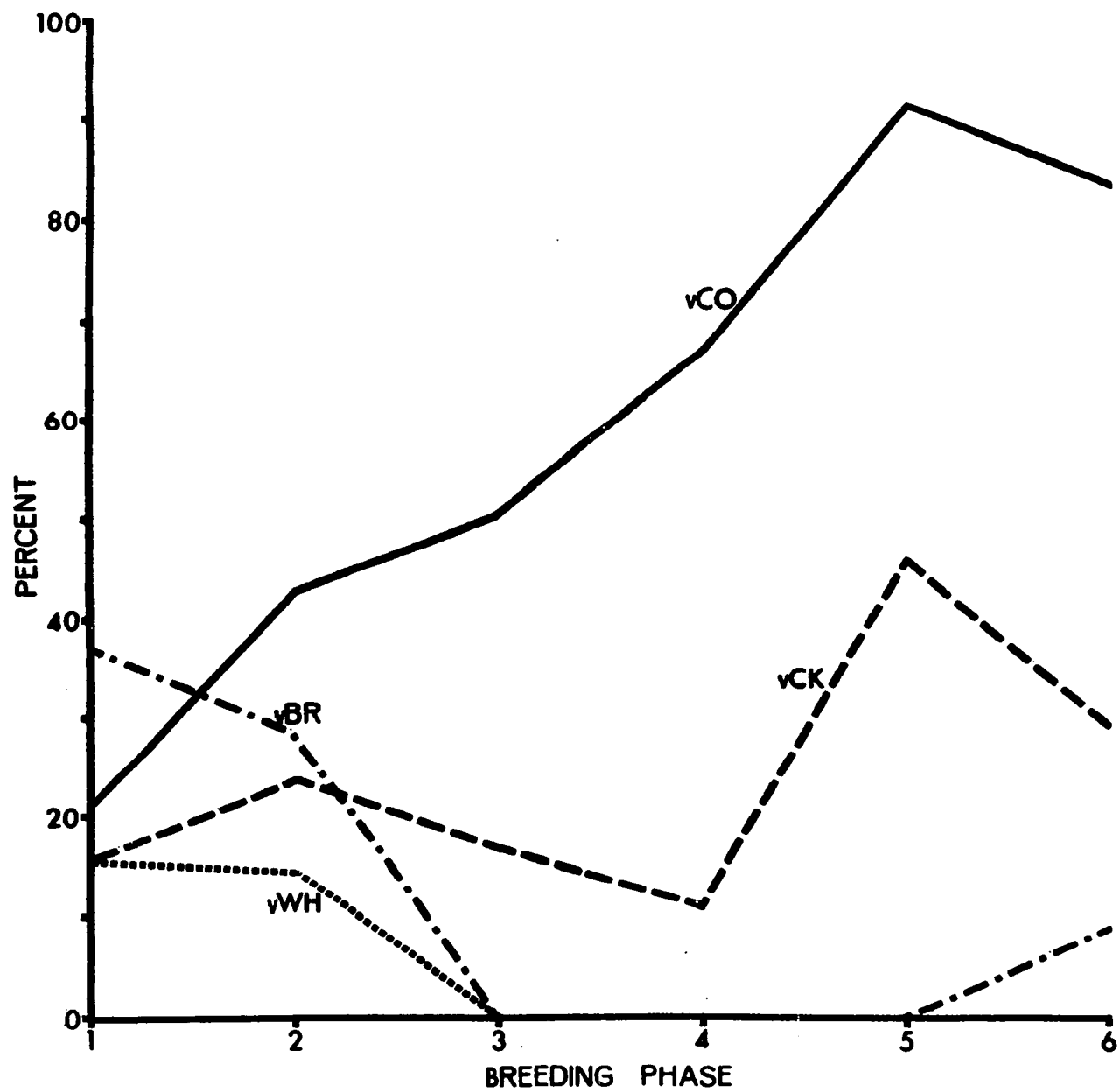
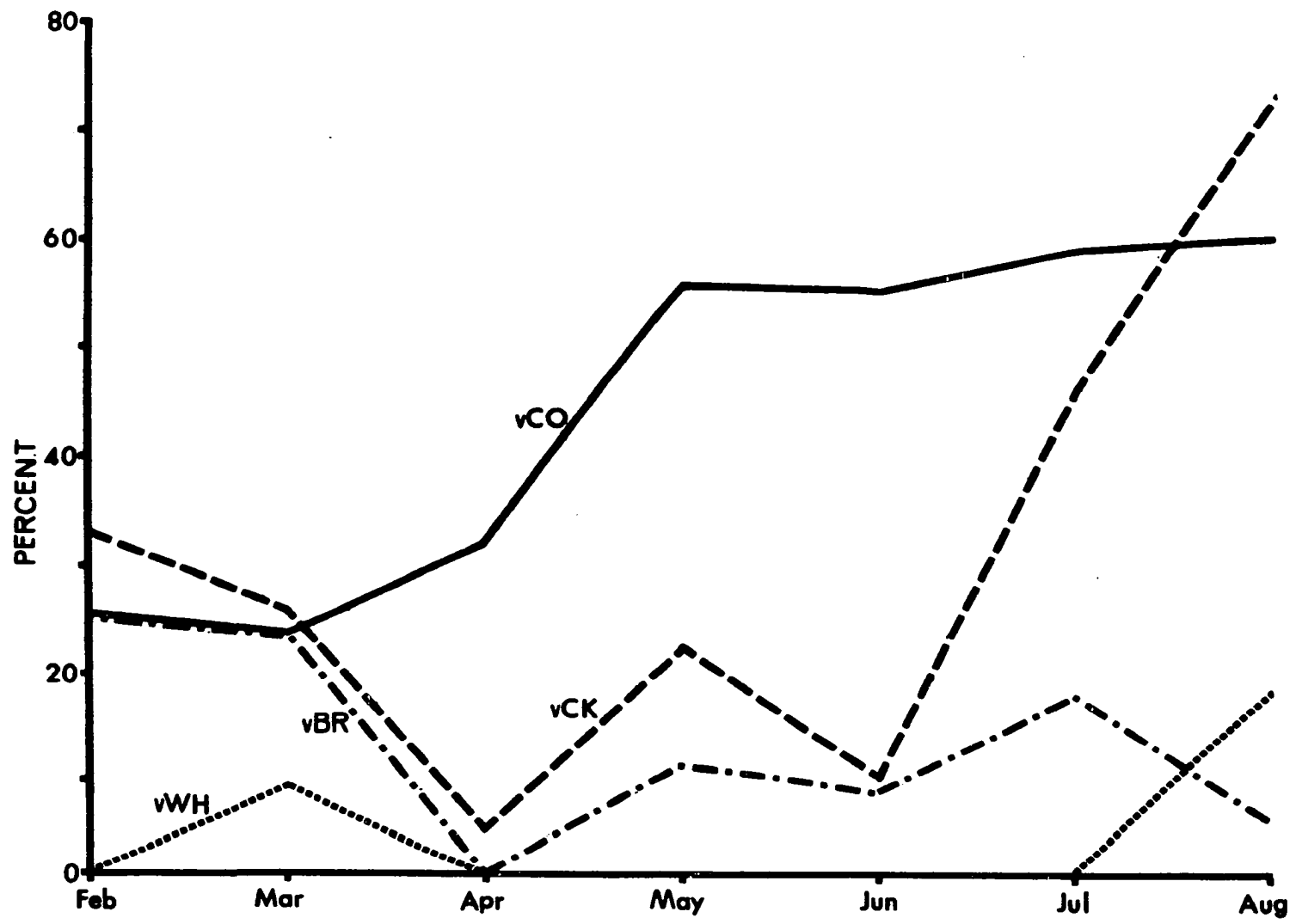


Figure 24. Acoustic responses of wild roadrunners to the vC0 playback throughout the breeding season at Big Bend National Park and South Texas sites.



naturally infrequent during BP3-5, but exhibiting high frequency during these phases in response to the test signal.

The responses of the captive breeding pair to the vCO and the vBR signals are presented in Table 14. A response pattern similar to that of wild birds was exhibited to the vCO, although without the diversity of responses exhibited in the wild. The pFK, pPR, pTW, pPN, and pFP responses were not exhibited by the captive pair, while the vGC was not exhibited by the wild birds. CM2, 3, and 4 exhibited vCO, pTW, pNMP, vWH, and vCK behaviors following presentation of the vCO, while CU1 gave only the vGC response.

In addition to eliciting the same responses from CM1 that the vCO had, the vBR signal also elicited pPR and vGC responses. (Table 14). On the other hand, CF3 exhibited a more limited repertoire to the vBR than to the vCO, omitting the pCH and vGC responses.

Table 14. Responses to the vCO and vBR playbacks by the captive breeding pair during the 1969 breeding season. Values represent frequency of each response.

Response	vCO Playback		vBR Playback	
	M	F	M	F
vCO	3		11	
vCK	2	3	1	5
pNMP	1		2	
vWH	1	1	1	1
pPR			3	
vGC		1	2	
vBR		4		6
pCH		2		
No. presentations	22	22	21	21

CHAPTER X

VISUAL STIMULI OF COURTSHIP AND COPULATORY BEHAVIOR

Introduction and Methods

Visual stimuli have been found to be critical cues in the courtship of many birds. In sexually dimorphic species males were found to mount and copulate a taxidermically prepared female specimen (Noble and Vogt, 1935; Lack 1940b; MacDonald, 1968) or part of the female body containing the critical anatomical structure (Schein and Hale, 1957), demonstrating the role of anatomical cues in sex recognition and stimulation of the male. For non-dimorphic species, on the other hand, behavioral differences provide recognition and stimulation cues (Nice, 1943; Collias, 1960). As the roadrunner lacks obvious sexual dimorphism, it was hypothesized that the male utilizes behavioral cues to identify females. The copulatory posture of the female roadrunner was tested for its ability to elicit courtship and copulatory behavior of the male. As the pTW display of the male was both a prominent preliminary and precopulatory behavior, it was hypothesized that the visual stimuli provided by head and tail movement in the display served in sex recognition and stimulation of the female.

The female copulatory posture model was prepared from a female skin, mounted in the appropriate position (Fig. 25ml). As the colors of the post-orbital patch faded a few days after death, oil base paint

was used to restore the color. A captive roadrunner was used to obtain accurate color definition. An artificial model simulating the pTW display was carved from balsa wood with features painted to resemble an adult with the post-orbital area fully exposed and ruffled crest (Fig. 25m2). The wings, tail, and crest feathers were from an immature male bird. The side-to-side tail movement (sector 4-5) was accomplished by a remote controlled battery-powered motor within the bird. The rate of tail wagging could be varied by the number of batteries in a series, and partial tail wags were possible by releasing the control switch. The head, under spring tension, was lowered to a bow by pulling a 40 m monofilament line and raised by slowly releasing the line. The degree and speed of the head bow and lift could be controlled by the tension on the line. The head and tail components of pTW display were presented alone or in combination, as well as presenting the model in a stationary position.

A male roadrunner skin, mounted in a non-courting position with wings held out from the body and fanned slightly, and the tail in sector B, was prepared as a control model. This position most closely resembled that of mild aggression (Fig. 25m3).

Each of the three models was presented to wild breeding pairs and to the captive pair. The models were presented to wild pairs 2, 3, 4, 5, 7, and 10 in their breeding territory during BP3-5 and to wild pair 1 during BP1. The pTW model was operated from behind shrubbery or from a parked car (6-10m away). In view of the ability of the vCO alone to stimulate courtship behavior (Chapter IX), each model was presented both alone and later in combination with the vCO playback. The responses to each situation were recorded, and compared with those

exhibited by these same breeding birds to the vCO alone (Chapter IX). The responses were frequently filmed with the Bolex movie camera (Chapter V) for detailed analyses.

Results

Because the behavioral responses of the wild roadrunners were similar for the three models, all model responses were combined in Table 15. The males exhibited courtship behaviors to all the models, but only when the vCO playback accompanied the model presentation. No males attempted copulation with a model, however. With the exception of the pTW response, which was exhibited to the model-vCO combination by slightly more males than in other situations, a greater percentage of the males exhibited the various courtship behaviors to the vCO alone than to the model-vCO combination. The female exhibited very little courtship behavior, with only the pFK (2 females) and the vBR (1 female) observed. The responses of WF8 account for the vBR and one of the pFK displays. In contrast to the males' responses, these courtship responses were given in the model-vCO situation, but not exhibited to the vCO alone. Notably lacking from the responses of these paired birds was the vWH which had been exhibited by several unknown birds in the vCO test alone (Chapter IX).

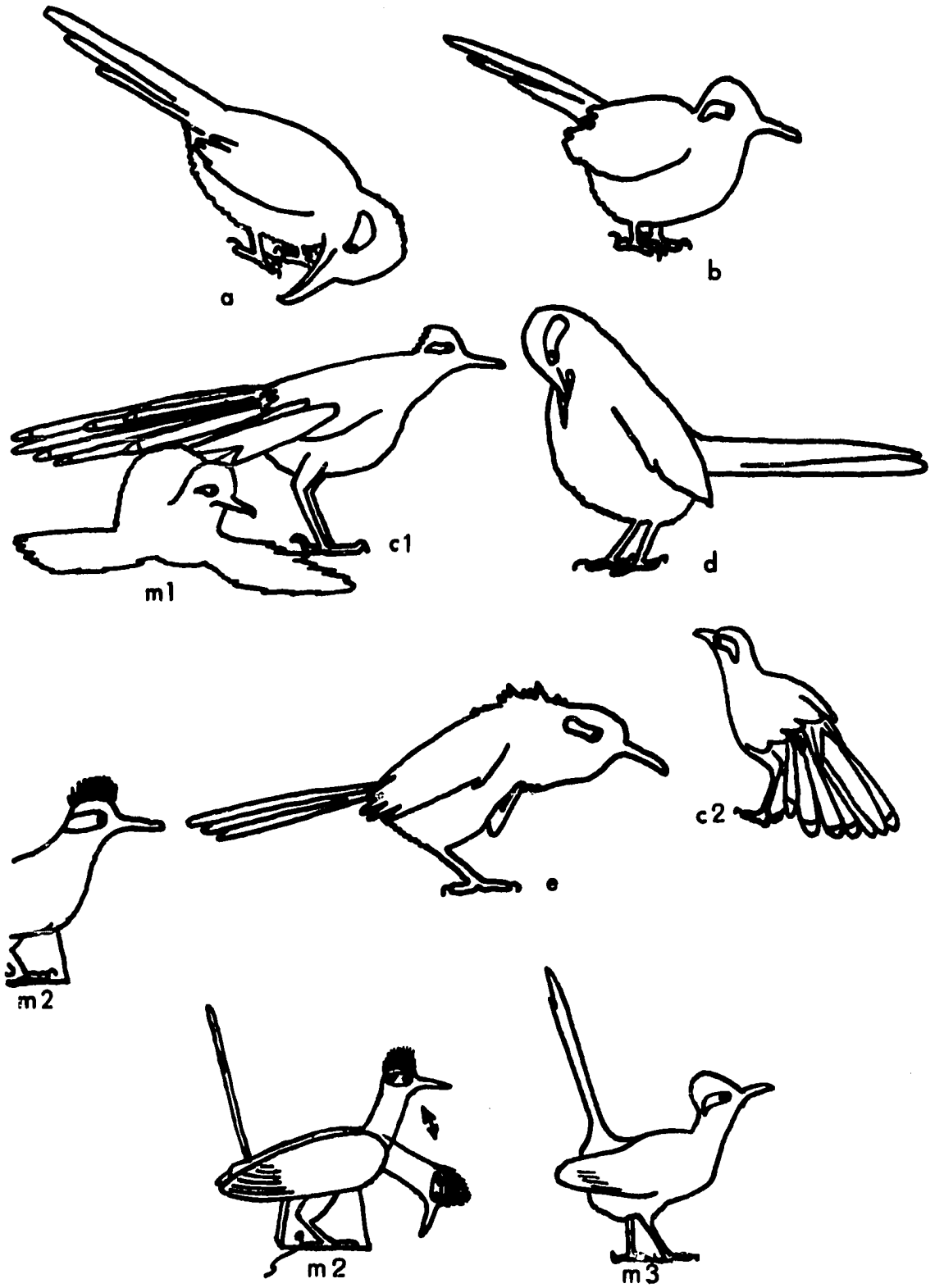
Both sexes exhibited several non-courtship responses to the model and model-vCO situation and less frequently to the vCO alone. The pBW was a rapid, jerky bill wiping on the substrate (Fig. 25a), similar to that exhibited after feeding. The preening (pPN) was a rapid, jerky preening motion, usually of the breast or flank feathers (Fig. 25d), and the head scratch (pHS) was a rapid scratching of the

Table 15. Responses of paired wild roadrunners to the vCO playback alone, to the model alone, and to the simultaneous presentation of model and vCO playback. Values represent per cent of the birds tested that responded.

Response	Model-vCO		Model		vCO	
	M	F	M	F	M	F
vCO	71.4				100.0	
pTW	57.1				50.0	
pPR	28.6				66.7	
pTW-ATT	57.1					
vSCO	14.3					
pBW	28.6	37.5	66.7	50.0		
pPN	14.3	50.0	66.7	50.0	16.7	16.7
pFP	14.3				16.7	
pFK	14.3	25.0				
vCK		50.0	33.3			33.3
vBR		12.5				
pCR		25.0		50.0		
pATT		12.5	66.7	50.0		
pCL	71.4	50.0	66.7	50.0		
Ignore		25.0		50.0		66.7
Birds tested	7	8	3	2	6	6
Presentations	16	8	5	4	18	18

Figure 25. Behavior exhibited by wild roadrunners near the experimental models.

- a. Bill wiping (pBW) by WM5.
- b. Crouching (pCR) by WF10.
- c. Circling and tail fanning by WF10.
- d. Preening (pPN) by WF10.
- e. Head scratching (pHS) by WM5.
- m1. Female model.
- m2. Artificial model.
- m3. Control model.



head with the foot (Fig. 25e). The pCR, a lowering of the body to ground or near ground level with sleeking of the feathers, was exhibited only by the female and only in the presence of the model (Fig. 25b). A frequent response of both sexes was pCL, a circling of the model with the tail moderately fanned and lowered to the ground, with sleeked feathers (Fig. 25c2). Periodically the tail side nearest the model was tipped upward, resulting in a ventral view of the white-tipped rectrices (Fig. 25c1). In the attack (pATT) the bird faced the model with wings drooped and tail forward (Fig. 8g), then ran at the model simultaneously fully fanning the tail and throwing it forward into sector A and throwing the fully fanned wings forward (Fig. 8h). The beak jabbed at the model's body, especially the head and neck areas, often tearing out feathers. This same display was exhibited in mirror fighting by wild birds. Males exhibited pATT only to the model alone, while females exhibited it in both model-vCO and model alone situations, though more frequently in the latter. During the above behaviors the crest was sleeked and the post-orbital area fully exposed.

The pTW-ATT response involved a rapid alternation from the pTW display to the pATT display for long periods of time, occasionally for several hours. This behavior was exhibited only by males in the model-vCO situation, and was often accompanied by the pBW, pPN, and pHS behaviors. The vSCO was given frequently by WM5 along with the pTW-ATT behavior. This was the only occasion in which this signal was heard in the wild.

The captive pair did not exhibit courtship behavior to any of the

models nor to the model-vCO situation. CF1 exhibited pCL, pCR, pPN, and pATT behaviors to the model, while CM1 exhibited only pCL.

CHAPTER XI

COURTSHIP COMPONENTS EXHIBITED BY JUVENILE ROADRUNNERS

Introduction and Methods

Juveniles of some avian species have been observed to exhibit components of courtship behavior that are not normally seen in their entirety or in proper context until sexual maturity. The most common example is the subsong of juvenile male passerines, exhibited during their first summer or fall (Lanyon, 1960). The purpose of this aspect of the research was to observe the ontogeny of motor patterns and acoustic signals of courtship and the context in which they first occurred.

Observations were made of seven hand-reared birds, five of which, CM1, 2, 3, CF1, and CU2, were taken from the wild as nestlings when 5-15 days of age and reared in pairs or groups of three in captivity (Chapter III). These birds had limited experience as early nestlings with the natural environment and with their parents. CM4 was artificially hatched and completely isolated from other roadrunners during development. SU1, obtained from the wild as a 9 day old nestling, was hand-reared in a semi-wild condition, maintaining some daily contact with his parents and siblings.

Ten wild young were observed as nestlings and fledgling: 3 young of W1 observed from 30-91 days of age; 4 young of W6 observed from 1-23 days of age; and 3 young of W2 observed from 1-38 days of age.

The wild young fledge when from 18-20 days old and remain with their parents until at least 50 days old.

Observations of the captive and wild young were supplemented with 16mm films of their behavior.

Results

The ages when the various courtship components were first exhibited by the wild, captive and isolated young are presented in Table 16. The wild young exhibited behaviors similar to those of adult courtship, with only pPR, pPC, and copulation not being observed. The pTW consisted only of the tail wagging and head bowing motions, without the vWR being given. Often during the vWH, the sound itself was omitted, with only the head motions observed. The pTW, pFK-B, pFK, and pNMP were exhibited to a parent and also to CM2 when he was released at site A. vCO, vBR, and vCK signals were given when the juvenile was alone and unattended by a parent. The vCK and vGC were given in response to the same signal by a nearby parent. Inter-sibling signals were limited to the vGC and vCK. The vICO was given along with the pFK-B to a parent or to CM2. The pFK and vWH responses were given following attack by a parent or when the threat of parental attack was present. pNMP was exhibited both to the parent, to CM2, and to siblings. On one occasion pNMP was exhibited by a juvenile while he also exhibited pTW to an adult. The control of crest erection and exposure of the post-orbital patch was first exhibited in conjunction with the vCK of the nestling, usually when a new stimulus appeared in the immediate environment of the nest.

The relatively few acoustic signals exhibited by captive juveniles

in comparison with the wild juveniles was the major difference noted between the two groups. The vCK and occasionally the vWH were the only acoustic signals of the captive juveniles. The isolate CM4 exhibited the vBR, but only on one occasion. The vCK, crest erection, and post-orbital area exposure occurred when the juvenile was placed in a new situation or confronted a new stimulus. The pTW consisted only of the tail wagging component, and was exhibited only while a juvenile was vigorously begging for food, accompanied by the begging call (Fig. 6a) and wing flapping (Fig. 18d). CM1, CF1, and CU1 exhibited this pTW behavior. The pFK and pNMP were oriented to humans and to siblings. The vWH and pFK were exhibited to humans in a manner similar to that of wild juveniles when attacked by their parents, although the captives were never attacked by the human.

Chasing of one another was a common behavior pattern seen both in captive and wild juveniles. The chase was similar to that described for preliminary courtship of adults, neither containing agonistic components. In addition, the wild young were often chased and attacked by their parents, although no physical damage occurred.

Table 16. Occurrence of components of courtship behavior in juvenile roadrunners. The age of the juvenile when the behavior was first exhibited is expressed in days.

Behavior	Wild Young	No. *	Captive Young	No. *	Isolate
vCK	8	10	8	5	8
vCO	37	2			
vBR	35	2			33
vGC	34	3			
vICO	70	2			
vWH	35	5	22	5	23
pTW	35	2	30	3	
pFK	34	2	32	5	20
pFK-B	70	2			
pNMP	23	6	23	5	22
Crest movement	12	10	12	5	12
Post-orbital area exposure	12	10	12	6	12
No. observed		10		6	1

*Indicates number of young birds exhibiting the behavior.

CHAPTER XII

DISCUSSION AND CONCLUSIONS

Functions and Derivations of Courtship Behavior

Various functions have been postulated for the elaborate and lengthy preliminary courtship exhibited by many avian species. Undoubtedly preliminary behaviors facilitate pair bond formation for they are not exhibited by avian species which meet only for copulation and maintain no subsequent contact. That pair-bond formation and maintenance are primary functions of the various preliminary behaviors of the roadrunner is supported by the observations that the roadrunner pair remains together throughout the breeding cycle, is often double-brooded, and exhibits a resurgence of preliminary courtship prior to renesting. The long preliminary courtship also may be necessary to insure sexual recognition in non-dimorphic species such as the roadrunner. As no evidence of territoriality by the roadrunner was observed prior to pair formation, the pair may be establishing the nesting territory as they forage together in the preliminary breeding phases. In areas where G. californianus and G. velox are sympatric, the differences in preliminary behaviors between the two may promote species distinctiveness. Marler and Hamilton (1966) postulate that an initial species-specific courtship insures reproductive isolation of the species.

A primary function of the elaborate visual and acoustic displays

that characterize precopulatory behaviors of most avian species is the synchronization of the reproductive physiology and behavior of the pair (Marler and Hamilton, 1966). The male's display, usually the more elaborate, promotes receptivity of the female, while the female's display indicates her readiness for copulation. That the male roadrunner's precopulatory display was directed toward inducing female receptivity was indicated by the prominence of the display following unsuccessful copulations as he pursued the female. That a male could not be stimulated to mount during the model experiments, even though he exhibited precopulatory displays, suggested that the cue indicating female receptivity was absent. Another function of the precopulatory displays is the maintenance of reproductive isolation of the species, especially in those species which lack preliminary courtship.

Avian courtship behaviors have been observed to reflect not only sexual tendencies, but also tendencies to attack and to escape from the mate (Hinde, 1953). Thus, another function of both preliminary and precopulatory courtship is the reduction of normal intraspecific hostile behavior (Dilger, 1956).

The derivation of most avian courtship displays is assumed to be from these sexual, aggressive, and escape tendencies (Bastock, 1967). Ritualization of intention movements (incipient or incomplete movements) of aggression and escape has long been recognized as the source of many courtship displays (Daanje, 1950). That aggressive tendencies are closely aligned with courtship in the male roadrunner was exhibited by the frequent alternation between the pTW display and model attack. The female was never similarly attacked, however. Components of the roadrunner courtship whose form suggested agonistic derivation were the

vertical, fanned tail position during pTW by the male, and the crest ruffling and pCH by both sexes. Flee tendencies were evident in the pPC, pFK, and pFK-B by both sexes, and the pPR by the male.

Other suggested sources of courtship displays are parental behavior, nest building movements, infantile behavior, and alerting postures (Andrew, 1961). pNMP and vWH head movements resembled nest building movements of the roadrunner, while courtship feeding and the head bowing of the male with food during pTW suggested parental behavior. None of the courtship behaviors appeared to be derived from infantile or alerting behaviors of the roadrunner.

The functions and derivations of the various visual displays of courtship are discussed more thoroughly in the following paragraphs.

Crest Ruffling and Post-orbital Area Exposure

The prominent display of the brightly colored post-orbital area during preliminary and precopulatory courtship of the roadrunner suggests that it is possibly a species recognition cue. The prominent display of such brightly colored species-specific structures is common in avian courtship (Tinbergen, 1948). This same area is red rather than orange in *G. velox*, and possibly developed as a reproductive isolating mechanism during sympatric speciation. This area may also be a cue for sex recognition. Although there was no sexual color difference, the greater frequency of exposure by the male could aid in sexual discrimination.

Crest ruffling in many avian species is an agonistic display, serving to increase the size of the bird during attack (Dilger, 1956). Crest ruffling causes the roadrunner head to appear much larger than

normal as the major crest feathers are greatly enlarged. Friedman (1933) reports crest ruffling during courtship by Tapera naevia, in the same sub-family with the roadrunner. The derivation of crest ruffling is suggested by Morris (1956) to be a ritualization of an autonomic pilomotor response in thwarting situations. This is usually in the form of a fluffing of the contour feathers during courtship, but ritualization may have resulted in the restriction of piloerection to special areas of the body, enlargement of these particular feathers, and the addition of color to the erected area. Such ritualization has occurred in the roadrunner's crest ruffling, correlated with the absence of contour feather fluffing during courtship. The orange post-orbital patch is spatially adjacent to the crest, and although its exposure was not dependent on crest ruffling, the two usually occurred simultaneously during roadrunner display. In addition, the conspicuous head movements of the pTW display of the male served to present the top of the crest and the orange area to the female. A similar correlation between conspicuous coloration and movements of the displaying bird has been reported for the courtship of several species, notably the blue-footed booby, Sula nebouxi (Armstrong, 1947).

Nest Material Presentation (pNMP)

pNMP, most prominent during nest building phases and nest site selection, apparently functioned to stimulate and synchronize the nest building efforts of the pair. On the numerous occasions in which the captive pair abandoned their nest and rebuilt, there was a resurgence of pNMP in their courtship. In the wild the continued occurrence of pNMP during incubation correlated with the observation that construction

of the nest lining was not complete until the eggs hatched. The increase in pNMP during RP6 was in association with renesting. Since pNMP also was exhibited long before nest building as one of the earliest interactions between birds, its role in pair bond formation is suggested.

pNMP was occasionally given in place of pFP by the captive males when food was not available, and the lack of food would possibly explain its use in pTW display during the latter phases of the wild breeding cycle. During the breeding season a captive male that was exhibiting pTW would not approach the human until he had found a stick to carry. The presence of an object in the bill might reduce aggression in the mate.

pNMP has not been reported in other cuckoo species, although it is a common avian courtship display (Tinbergen, 1952).

The female roadrunner does the majority of the nest building with the male bringing the twigs up to her. During nest construction she will often give the vWH, especially when the male is nearby but has temporarily abandoned his role of twig provider. This is usually followed by renewed twig gathering by the male. Prior to actual nest construction this same pattern was seen, with the female giving the vWH from a shrub or tree, and the male responding with pNMP. Tinbergen (1952) interprets such behavior occurring before nesting as a ritualized displacement behavior. The head movements accompanying the vWH appear to be derived from the movements of nest construction.

Chasing (pCH)

That the pCH was one of the earliest interactions between the

sexes and that it occurred not only in BP1 and BP2, but also in BP6 in association with reneating suggest a pair formation and maintenance function. Although some chases observed may have been territorial, the occurrence of other courtship behaviors in association with the pCH indicates a primary courtship function.

The sexual chase is a common avian courtship behavior, although it is usually aerial. Sexual chases are thought to be an expression of sexual motivation that would otherwise be directed to copulation, or an expression of aggression (Marler, 1956b). The observation that no copulation occurred during the pCH of the roadrunner suggests that it served as an outlet for the high copulatory motivation of the male until normal expression was possible later in the breeding cycle. During BP6 the pCH by the male correlated with the highest frequency of refusals to copulate by the female for any breeding phase.

Prancing (pPR)

The pPR and associated vPOP were rarely exhibited by a paired wild male, and then only in the presence of his mate. However, it was a relatively frequent response to the vCO playback, occurring in association with the vCO and pTW responses. Based on these observations and the fact that the pPR recurred in CM1 whenever the pair bond was broken, it is suggested that the pPR functions in early pair formation. The loudness of the vPOP, the prominent movements, and the occurrence in the vCO playback experiment, but not in the model-vCO situation, suggest it serves primarily as an attractant display.

The components of the pPR display appear to be derived from a flee tendency. A vertical tail position is considered to be derived from

the flight intention movement (Daanje, 1950). Also, the displaying bird always ran from the mate or sound source.

During the pPR and pFK display the tail is not fanned, in contrast to other displays in which the tail is held in the vertical position (pTW and attack positions). This suggests that the tail-raising may function to display the white tips of the rectrices, for during pTW and pATT the displaying bird faces the partner, and in this position the spots would not be visible unless the tail were fanned. However, during the pPR and pFK displays the rear view is presented to the partner, and fanning is unnecessary to reveal the white tips of the rectrices.

A similar aerial display with accompanying noise has been observed in the male spruce grouse, Canachites canadensis, where it was thought to serve a territorial function (MacDonald, 1968). Some species of hummingbirds exhibit an aerial wing popping thought to function as a sexual attractant (Busnel, 1963).

Tail Wagging (pTW)

The pTW presents a variety of stimuli simultaneously to the female: a rhythmic tail motion, movement of the head, the patterning of the white tips of the rectrices, and the vWR call. That this display usually preceded copulation suggests its function in promoting female receptivity and possibly in stimulating ovulation. Only occasionally was the pTW omitted in the precopulatory situation, and then only in birds that had been paired for some time. It was the most frequent courtship display of the male following an unsuccessful copulation.

The fanned tail in the vertical or near vertical position during

the pTW closely resembled the attack posture of the species. This behavior resulted in the bird appearing larger than normal, a situation characteristic of agonistic displays. Thus an aggressive derivation is suggested for the tail component of the display. The vertical position of the tail is usually considered to be a flight intention movement, indicating either the tendency to approach or flee (Daanje, 1950).

The head bowing component of the pTW resembled the head bowing seen in passerine courtship. Among passerines this movement is thought to be derived from the placement movements of nest building or feeding the young (Andrew, 1961), although these latter movements of the road-runner do not resemble its head bowing. The only other behavior in which the head is bowed was while the vCO or vSCO were given, and these movements possibly share a common origin with the head bowing of the pTW display. During head bowing the post-orbital area is prominently displayed, suggesting that this is one of the primary functions of head bowing.

A similar display involving tail wagging, crest erection, and conspicuous wing movements, but lacking the head bowing, was described for Tapera naevia (Friedman, 1933). The courting male Inca dove, Scardafella inca, which possesses a white-tipped rectrix pattern, displays with tail raised and fanned (Johnston, 1960).

Female Precopulatory Behavior

As the female consistently exhibited rear presentation and pFK prior to successful copulation, these behaviors are undoubtedly cues indicating her sexual receptivity. The pFK variation exhibited by the

captive female and one wild female prior to unsuccessful copulations possibly indicated non-receptivity, for the captive male would rarely attempt mounting in this situation.

The pFK was given not only by the female in the precopulatory situation but also by both sexes throughout the year. It most often occurred as another roadrunner approached or as a strange object was encountered. The captive female exhibited the pFK more frequently, both during the year and as a juvenile. The situations in which it occurred during the non-breeding season suggested that it was an appeasement behavior, designed to prevent attack by reducing aggression in the approaching bird. The tail and wing flick components were similar to those exhibited by many species in similar situations and are thought to be derived from flight intention movements (Andrews, 1961). The pPC and pFK-B displays were similar to the pFK, and all occurred in situations where a reduction of aggression in the partner would be warranted, i.e., when the pair was in very close proximity. The rear presentation movement may have been derived from an escape intention movement.

Hamilton and Hamilton (1965) reported a precopulatory display of the female yellow-billed cuckoo, Coccyzus americanus, similar to an exaggerated flight intention movement with the tail straight up. A rapid series of tail flicks by a female C. americanus was observed preceding copulation (personal observation).

Postcopulatory Display (pPC)

Postcopulatory displays are reported for relatively few avian species, being most widespread in the Anseriformes (Johnsgard, 1965).

The adaptative significance of postcopulatory displays is not clearly understood, since selection pressures are usually exerted on behaviors that precede copulation. Maintenance of the pair bond and prevention of aggression between the pair following copulation are proposed functions. Observations indicate that postcopulatory displays occur more commonly in species such as the roadrunner that maintain a pair bond and where both parents share nesting duties. The similarity of the pPC to the pFK and pFK-B support a reduction of aggression function, also. The VICO of the pFK-B and the pPC also sounded identical to the human observer, although recordings and analysis of this call were not possible in this study.

Courtship feeding

Courtship feeding by the male roadrunner was reported by Rand (1941) and Calder (1967). Both authors, however, described food exchange as occurring after copulation, whereas film analysis revealed that in both wild and captive copulations, food exchange occurred at the time of cloacal contact. Rand (1941) reported that the female turned her head for the food rather than raising it as reported in this study.

Courtship feeding has been reported in other cuckoos, including the yellow-billed cuckoo, Coccyzus americanus (Hamilton and Hamilton, 1965), black-billed cuckoo, Coccyzus erythrophthalmus (Spencer, 1943), Centropus javanicus (Lack, 1940a), and the squirrel cuckoo, Piaya cayana (Skutch, 1966). These species all share the solitary, non-parasitic nesting habit with the roadrunner. In contrast to passerine and galliform courtship feeding, which occurs prior to copulation (An-

drew, 1961; Stokes and Williams, 1971), food exchange occurred during copulation in these cuckoo species.

The most obvious function of courtship feeding is to induce receptivity in the female (Stokes and Williams, 1971). However, the fact that successful copulations occurred without food in the roadrunner suggests that food presentation is not essential to stimulate female receptivity. During pair formation this function may be more important than later in the season.

Another function of courtship feeding is the maintenance of the pair bond, especially in those species where both sexes care for the young. Lack's (1940a) survey of courtship feeding in birds revealed its occurrence primarily in species in which parental duties were shared. Among galliform polygynous species, courtship feeding ends with egg laying; whereas in monogamous species which share nesting duties, it often continues throughout the breeding cycle (Stokes and Williams, 1971). The pair bond maintenance would be essential in the roadrunner which shares parental duties and often renests.

It has also been suggested that courtship feeding provides nourishment to the female during egg laying, although Lack (1940a) has dismissed this function for most species. However, the nature and large size of the roadrunner courtship food (reptilian), differing from the normal insectivorous adult diet, indicate a nutritive function. Supporting this view are the observations that most courtship food was consumed by wild females just prior to and during egg laying and that the captive female consumed more food during egg laying periods.

Courtship feeding in the roadrunner may also serve as an indicator of the favorability of the environment for nesting. A successful

roadrunner nesting is dependent on a large supply of reptiles in the breeding territory, and courtship feeding may supply information on the nature and quantity of appropriate food. Thus the female may not lay eggs until the proper stimulation in the form of courtship food is provided. The synchronization of nesting and abundant food supply would thus be insured early in the breeding season. Following the first nesting, the quantity and quality of the courtship food would determine whether renesting occurred.

A possible secondary function of food exchange in the cuckoo group, in which it occurs during cloacal contact, is as a balancing aid for the male. The male roadrunner exhibited difficulty in balancing during cloacal contact, evident by vigorous wing flapping. It was during this time that both sexes were grasping the food, possibly giving the male additional support. This function was suggested for Piaya cayana when it was observed that the long cuckoo tail was a detriment to proper balance (Skutch, 1966). Although the male roadrunner was able to balance himself by wing flapping during copulations in which no food was involved, adequate cloacal contact may not have occurred. On one occasion when no food exchange was involved, WM2 grasped the head of the female during cloacal contact. Brockway (1964) reported a similar grasping of the female's head correlated with balancing during copulation in the budgerigar (Melopsittacus undulatus).

Associated with courtship feeding in most passerine species is a female display and call resembling the food begging of the young of that species, leading to the suggestion that courtship feeding has evolved from the general parental feeding behavior (Lack, 1940a, Armstrong, 1947). Rand (1941) and Calder (1967) observed such an infan-

tile behavior in the female roadrunner associated with courtship feeding, consisting of wing fluttering and the buzzing call of the young. This behavior pattern was never observed in the captive or wild adult females during the present study. The call of the adult roadrunner that most closely resembled the nestling begging call was the vWH, although the posture accompanying the vWH did not involve wing fluttering or other infantile behavior. An infantile female courtship display has not been reported in other cuckoos nor in galliform species that exhibit courtship feeding (Stokes and Williams, 1971). The posture and acoustic signal of the male roadrunner was not similar to the parental feeding behavior of the species. Thus, if courtship feeding in the roadrunner has parental or infantile derivations, its present nature has resulted from considerable modification of the derivation source.

Acoustic Signal Functions

Roadrunner acoustic signals reported prior to this study were the vCO (Holterhoff, 1883), vCK (Sutton, 1922), and vWR (Calder, 1967). The vCK was assumed to be an alarm signal and the vCO a male love call (Sutton, 1940).

The variety and prominence of acoustic signals in roadrunner courtship, especially during preliminary phases are not surprising when one considers its ecology. Acoustic signals would be more effective than visual signals as initial attractant and orientation signals in species with low population densities and exhibiting solitary habits. The cursorial habit also favors the use of acoustic rather than visual signals for initial attraction. On the other hand, aerial courtship displays are common attractant signals in the courtship of aerial species.

The lack of anatomical cues for sexual recognition favors the use of acoustic and other behavioral differences to facilitate sexual discrimination. This research strongly suggests that the vCO, vWR, and vPOP are exclusively male signals, the vBR and vWH are primarily female signals that are given only rarely by males, and the other signals are exhibited equally by both sexes.

During this study information on the functions of the various courtship calls was derived from various lines of observational evidence, and also from experimental evidence in the case of the vCO. In the following paragraphs the functions of the various acoustic signals will be discussed.

The physical characteristics of signals can serve as clues to their function (Marler, 1966). Based on intensity, the roadrunner signals fell into two groups: those that were loud and carried great distances in the field (vCO, vCK, vBR), and those that were soft and carried only short distances. The former type would serve as attractant and orientation signals between potential pair members (Busnel, 1963). That these calls were most often given when the bird was alone supports this view. Among passerines the attractant signal is more often given by the male when alone than when in the presence of the female (Andrew, 1961).

The frequency characteristics of the various signals exhibited little variation, all being low in frequency. Since low frequency calls are perceived at greater distances than are high frequency calls of the same intensity, the low frequency calls used in establishing contact between widely spaced birds would be an adaptation to low population density.

Temporal characteristics of the signals varied slightly. Those calls with sharp, repeated breaks in sound and with short notes and short intervals between notes convey information about position of the calling bird, while long, monotonous notes are difficult to localize in the environment (Marler, 1956a). The vBR and the vCK exhibit the physical properties that facilitate localization. Even though not possessing these physical properties, however, a call that is repeated for long periods of time with the bird remaining fixed can facilitate localization (Busnel, 1963). The behavior of a male when giving the vCO is an example.

The frequency of occurrence of the signal during the various breeding phases gives information about its function. It was seen that the vBR, vCO, and vCK, for which an attractant and localization functions are proposed, were much more frequent during the early breeding phases than were the softer calls. Later in the cycle these calls were not as frequent, with the exception of the vCK. Decrease in calling by males following pair formation has been reported for many avian species (Collias, 1960).

Communication patterns also supply information concerning functions of acoustic signals. The three loud calls, vCO, vBR, and vCK, were most often given when the roadrunner was alone, supporting the attractant and localization functions. Similarly, territorial calls were most often given by solitary birds, with mutual calling often serving as a substitute for actual combat between males.

The response patterns between known paired birds would function in maintaining the pair bond, synchronizing the behavioral and physiological aspects of copulation, maintaining contact between the pair

when separated, and recognition of the mate (Marler, 1956a). Frequent patterns that occurred when the pair was separated were vCO-vCK and vCK-vCK. The most common of these was the vCK-vCK, suggesting that it is the most important call in maintaining pair contact. When the pair was together, the communication patterns would function in reducing hostile tendencies and promoting copulatory behavior. These patterns included vGC-vGC and vCK-vCK.

The results of the vCO experiment support the attractant and localization function of this signal. Birds that exhibited both male and female behaviors were attracted to the vCO playback, often giving an acoustic response at distances greater than 50 m away and then gradually moving closer to the sound source. That birds were not only attracted to the vCO but also exhibited male and female preliminary and precopulatory behaviors indicates that the vCO also functions in stimulating sexual behavior in both sexes.

Hamilton (1965) reported that when the loud, characteristic call of the yellow-billed cuckoo was played back to wild birds, it served as an attractant and orientation signal in this widely spaced species.

A territorial function for the vCO was not indicated in this study. When a call is territorial, males will usually respond to a playback of the call with aggressive displays, and if a model is presented will attack it (Dilger, 1956). As the roadrunner males never exhibited aggressive displays to the vCO alone or to the model-vCO presentation, the territorial nature of the vCO was not substantiated.

The fact that the vBR was never associated with any of the male courtship displays in response to the vCO playback indicates that it was given primarily by the females. Only the captive pair was pre-

sented with the vBR playback, and results indicated that the vBR stimulates sexual displays in the male, but not in the female.

The vWR was the call that consistently preceded copulation, and undoubtedly functioned to induce receptivity in the female. Also, it served to promote physiological readiness for copulation. A male pre-copulatory vocalization presented alone was found to stimulate egg-laying and ovulation in female budgerigars (Brockway, 1965). That the vGC also functioned to induce female receptivity was indicated by its frequent production by the male as he pursued the female after an unsuccessful copulation. The vGC was also an important signal in inducing various behaviors in the nestlings and fledglings. The vICO, vPOP, and vWH were discussed with their respective accompanying visual displays in the previous section.

The physical characteristics of the vCO exhibited the greatest amount of inter-individual and intra-individual variation. Marler (1960) has suggested that such intra-population differences serve to identify individuals and aid in pair bond maintenance, while intra-male variation, by adding more cues, also aids in individual recognition of the mate. One would expect individual recognition in species where pair bonds last throughout the breeding cycle (Marler, 1960). It is proposed that the vCO of the male is an individual recognition signal, and that after pair formation the female responds only to the vCO of her mate. This view is supported by the absence of courtship responses to the vCO playback by the paired wild females, while female courtship behavior was exhibited by the general roadrunner population to the vCO playback. Thus the females that responded with courtship behaviors would be unpaired.

The sexual variation in temporal characteristics of the vCK that was observed in both a captive and wild pair may serve in sexual recognition, although more recordings and analyses are needed to verify this observation.

In other cuckoos a cooing sound (Coccyzus americanus, Hamilton, 1965; Cuculus canorus, Herrick, 1910; Eudynamys orientalis, Gosper, 1964) and a bill snapping noise (Piaya cayana, Morococcyx erthropygus, Skutch, 1966) have been reported.

Sexual Recognition

The results of the model experiments indicate that in the precopulatory situation the male roadrunner does not recognize the female on the basis of anatomical cues, for male courtship displays were exhibited to both the male and female mounted skins. That precopulatory behaviors but not mounting was elicited by all models indicates that the behavioral display signaling female receptivity was absent. From observations of the female precopulatory pattern, this cue is either the rear presentation, the pFK, or both. Apparently the male roadrunner, not having anatomical cues to identify the sex of another roadrunner, courts all roadrunners, and the subsequent behavioral response of the other bird identifies its sex. That paired males in all breeding phases courted the model indicates that either there is no individual recognition of his female by a paired male, or that the male is potentially promiscuous.

The observation that the model was courted only when the vCO playback accompanied it is difficult to explain. One possibility is that the vCO is given by the unpaired female, although it was not exhibited

by the captive female. Another possible explanation is that although the vCO is a male call, it stimulates other males as well as females. The process of giving his own vCO might also serve to stimulate sexual behavior in the male.

The responses of the paired females to the models revealed little information concerning sexual recognition. The fact that little or no courtship behavior was exhibited to the model suggested that either critical cues identifying the model as a male were absent, or that the female recognizes her mate and is monogamous.

Displacement Behavior

The pPN, pBW, and pHS behaviors exhibited to the models are all normal comfort movements of the roadrunner. In the model situation, however, each differed from its normal form in consisting of fast, jerky movements, and in being accompanied by post-orbital patch exposure. Such comfort movements are frequently displacement behaviors in a variety of organisms and have become ritualized as regular components of courtship in some species (Tinbergen, 1952). Ritualization of these displacement behaviors does not appear to have occurred in the roadrunner as these movements were never seen in the normal courtship. In the model situation the occurrence of displacement behavior indicated that the bird was in a situation where two conflicting drives were activated or that the same drive was activated and thwarted by the absence of the key releasing stimuli (Bastock, Morris, and Moynihan, 1953). The frequency of displacement behavior exhibited to the models supports the view that key stimuli for both the male and female were not supplied by the model.

Cyclic and Seasonal Patterns

One unusual feature of the breeding cycle of the roadrunner was the continuation of copulation after the need for egg fertilization no longer existed. This behavior undoubtedly facilitated pair bond maintenance and prepared the pair for renesting. Also correlated with renesting was the resurgence of preliminary courtship behaviors, especially the acoustic signals, during BP6. Although it cannot be assumed that all pairs renested every season, the results suggest that the potential for renesting is present, and will be expressed if the environmental conditions are favorable. The second peak in acoustic signals (Fig. 20) most likely corresponds with the potential for renesting in the general population. Observations on a wild pair during BP6, in which the male repeatedly courted the female unsuccessfully and no renesting occurred, suggest that the male is a potential renester regardless of the environmental conditions. Perhaps the female determines whether renesting will occur, based on the quantity of courtship food or some other environmental indicator.

Determinants of Behavior

The development of behavior within an organism is considered to involve a complex interaction between both genetic tendencies and experience with the environment (Lehrman, 1953), although the relative importance of each factor varies greatly in different organisms. In the roadrunner the appearance of all courtship behaviors in the isolate indicates a very strong genetic basis for these behaviors, although the role of self-stimulation and self-feedback cannot be completely ruled out. The stereotyped time-motion patterns appearing in captive and

wild birds also suggest genetic origins.

Although the motor patterns of courtship appear to be very stereotyped and genetically determined, the stimuli to which these behaviors were directed were very flexible, as indicated by the captive males that exhibited courtship displays to humans. This distortion in the choice of a mate resembles or is identical to the phenomenon of imprinting first reported in precocial birds (Lorenz, 1937). Imprinting occurs in species in which the young do not instinctively recognize adult members of their own species, rather a single exposure to the proper stimulus during an early, short critical period determines species recognition throughout the rest of life. One must be cautious in applying the term imprinting to altricial birds, however, for during their long dependency period species recognition may be accomplished by the normal conditioning process (Slukin, 1965). It may be concluded that species recognition is not instinctive in the roadrunner, but is determined by either imprinting or early experience.

The absence of most acoustic signals during the juvenile life of the captives was the major difference between captive and wild development. This result suggests that the potential for acoustic production is present during juvenile life, but that experience with the calls of their parents or other adults is necessary for the calls to be given by juveniles. This lack of early experience did not affect the adult calls of the captives, however.

CHAPTER XIII

SUMMARY

The courtship and copulatory behaviors of the greater roadrunner, Geococcyx californianus, were investigated at field sites in Texas and Oklahoma and in hand-reared captives. Observations, single-frame analyses of 16mm films, and spectrographic analyses of tape recordings provided descriptions of the sexual behavior of this species.

The reproductive cycle began with a lengthy preliminary courtship characterized by complex sequences of acoustic and postural displays by both sexes. The precopulatory and copulatory behaviors were highly stereotyped, sequential complexes of acoustic and postural displays, most prominently exhibited by the male. The precopulatory behavior usually included food presentation by the male, with the female taking the food during cloacal contact. Both sexes exhibited a postcopulatory display with a definite time-motion pattern. Sexual differences consistently occurred in the acoustic and postural displays of both captive and wild pairs. Presentation of male and female models in field experiments suggested that behavioral rather than anatomical cues functioned in sexual recognition and stimulation of copulatory behavior.

The courtship pattern of wild and captive pairs changes as the breeding cycle advanced. Preliminary displays were most prominent early in the cycle, subsided greatly with nesting, and became prominent

again during fledgling care. Copulation, first occurring in late pair formation, persisted throughout the cycle regardless of the need for egg fertilization. The male often omitted precopulatory displays during nesting, but again exhibited them during fledgling care. The re-nesting potential of the pair might account for these breeding cycle changes.

Nine acoustic signals were utilized during the breeding season, three of which were male-specific. All were simple, low frequency sounds or noises with a dominant frequency range of from .2-2 kHz, but of greatly varying intensities. Acoustic communication between distantly spaced birds involved the louder signals, while the softer signals were exchanged between pair members in close proximity. Field and laboratory experiments indicated that the coo, the prominent male call, served as an attractant signal for both sexes and also elicited preliminary and precopulatory displays of both sexes. Nesting females were exceptions as they did not exhibit attraction to or sexual stimulation by the coo playback.

Captive hand-reared males exhibited typical courtship and copulatory displays to humans, although the captive female did not. That these behaviors appeared in hand-reared birds and also in an incubator hatched male reared in species isolation indicated their strong genetic basis.

Certain motor patterns and acoustic signals of preliminary and precopulatory courtship appeared in captive and wild juveniles, although not in a sexual context.

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APPENDIX

Symbols Used in the Dissertation

Postural Symbols

- pATT Attack posture with tail fanned and held in the vertical position and the wings dropped and fanned (Fig. 8g-h).
- pCH Chasing behavior between the sexes, most prominent in preliminary courtship.
- pCL Circling an object with tail moderately fanned and lowered (Fig. 25c1, c2).
- pCR Crouching behavior, a lowering of the body to ground or near ground level with feathers sleeked (Fig. 25b).
- pFK Flicking of the tail upward, a precopulatory display of the female roadrunner (Fig. 10, 11, 12).
- pFK-B Flicking-bow display, exhibited by both sexes. A slight bowing of the body followed by a sudden, upward flicking (Fig. 15e-f).
- pFP Presentation of courtship food by the male roadrunner (Fig. 9e).
- pHS Displacement behavior, consisting of a rapid head scratching using the foot (Fig. 25e).
- pNMP The carrying of nesting material in the bill and presentation of it to the opposite sex, exhibited by both sexes.
- pPC Postcopulatory display exhibited by both sexes (Fig. 15a-d, 16).
- pPN Displacement behavior, consisting of rapid, jerky preening motions, usually of the breast or flank feathers (Fig. 25d).
- pPR Prancing display of the male roadrunner, possibly used as a sexual attractant stimulus (Fig. 8a-f).

- pTW Precopulatory display of the male roadrunner, consisting of a side-to-side tail wagging and simultaneous head bowing (Fig. 9).
- CP-S Successful copulation (Fig. 14).
- CP-U Unsuccessful copulation.

Acoustic Signal Symbols

- vBR A loud, barking call of from 2-22 identical notes, usually given by the female (Fig. 4a).
- vCK A loud, clacking call, which also has a noise component produced by the snapping of the mandibles (Fig. 5b). It is produced by both sexes and is the most common call of the roadrunner.
- vCO Courtship call of the male roadrunner, consisting of from 3-8 cooing notes (Fig. 1, 2a, b) and accompanied by pumping head movements (Fig. 17).
- vGC A soft, growling call given by both sexes, both in courtship and in parental behavior (Fig. 5a).
- vICO A soft, single cooing call accompanying the pFK-B and pPC displays.
- vPOP A loud, popping noise produced by wing movements during the pPR display of the male roadrunner (Fig. 8a-f).
- vSCO A soft call of 2-3 cooing notes (Fig. 2c, 3) given by the male with characteristic head movements (Fig. 18a, b).
- vWH A soft, whining call of one very long note (Fig. 6b) produced as the head is lowered and wiggled from side-to-side (Fig. 18c).
- vWR A soft, whirring call (Fig. 4b) accompanying the pTW display of the male.