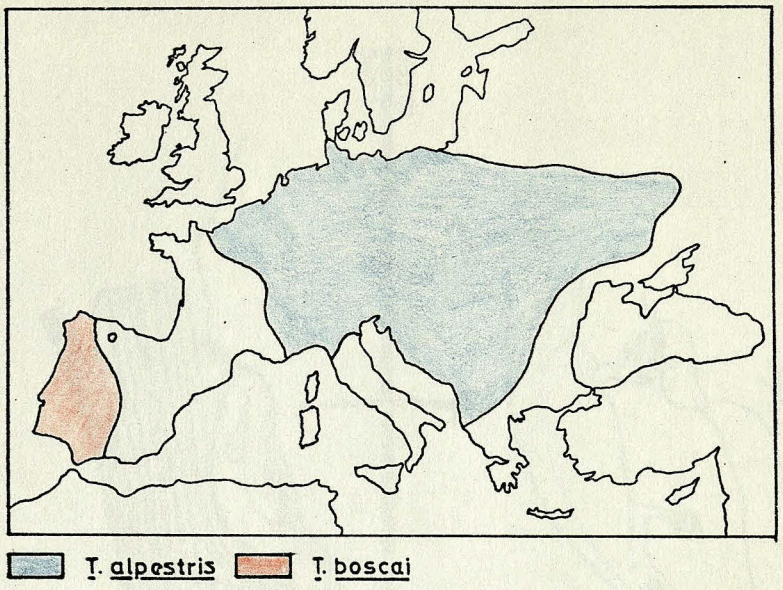
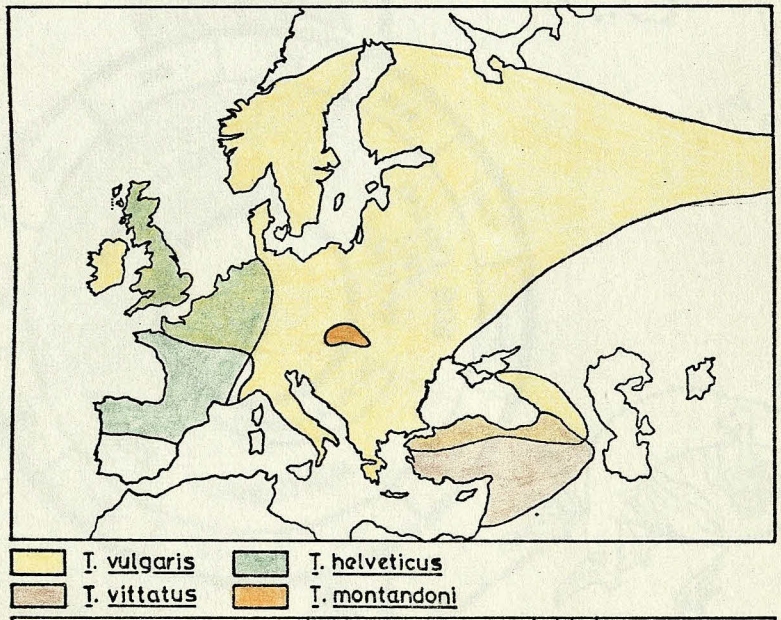
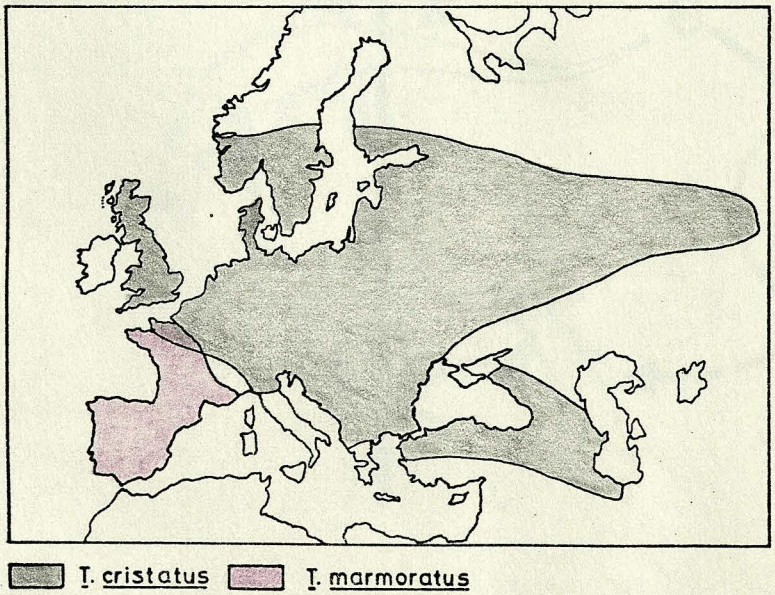


VOLUME 2

ILLUSTRATIONS







DISTRIBUTION OF Triturus spp.

After Steward (1969).

LIFE CYCLE OF SMOOTH NEWT, *Triturus vulgaris*.

LIFE CYCLE OF SMOOTH NEWT, T. vulgaris.



FIG A: A male swimming.



FIG B: A male showing toe clipped for marking purposes.

THE SMOOTH NEWT, T. vulgaris.

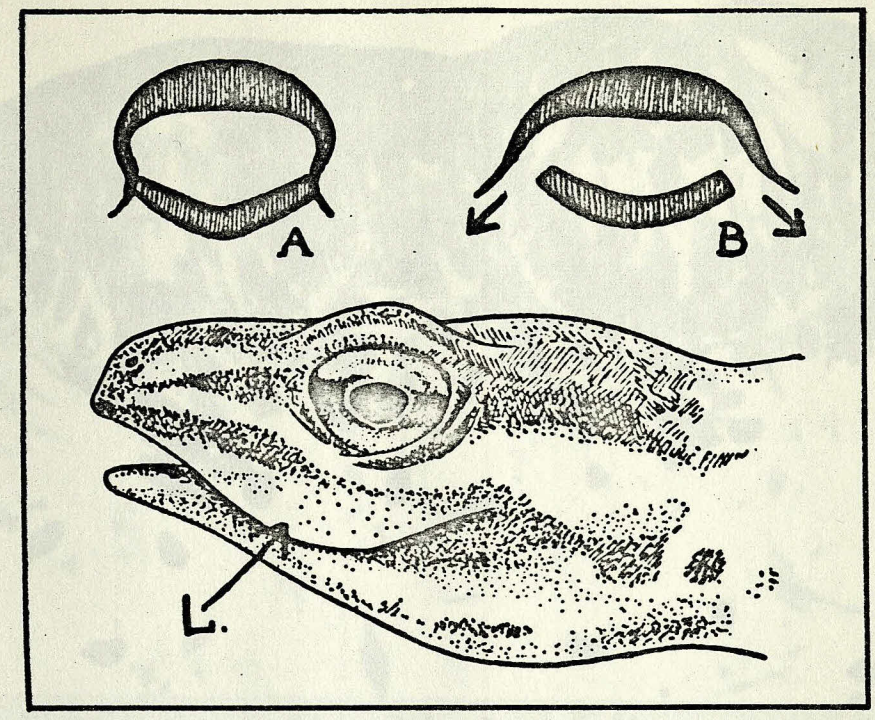


FIG A: L: extended upper lip, A: mouth opening, B: mouth closing. A and B are transverse sections.

Reproduced from Tinbergen and Ter Pelkwijk (1938).



FIG B: A female Palmate Newt, Triturus helveticus.

ADAPTATION FOR AQUATIC LIFE

MODIFICATION OF THE UPPER LIP

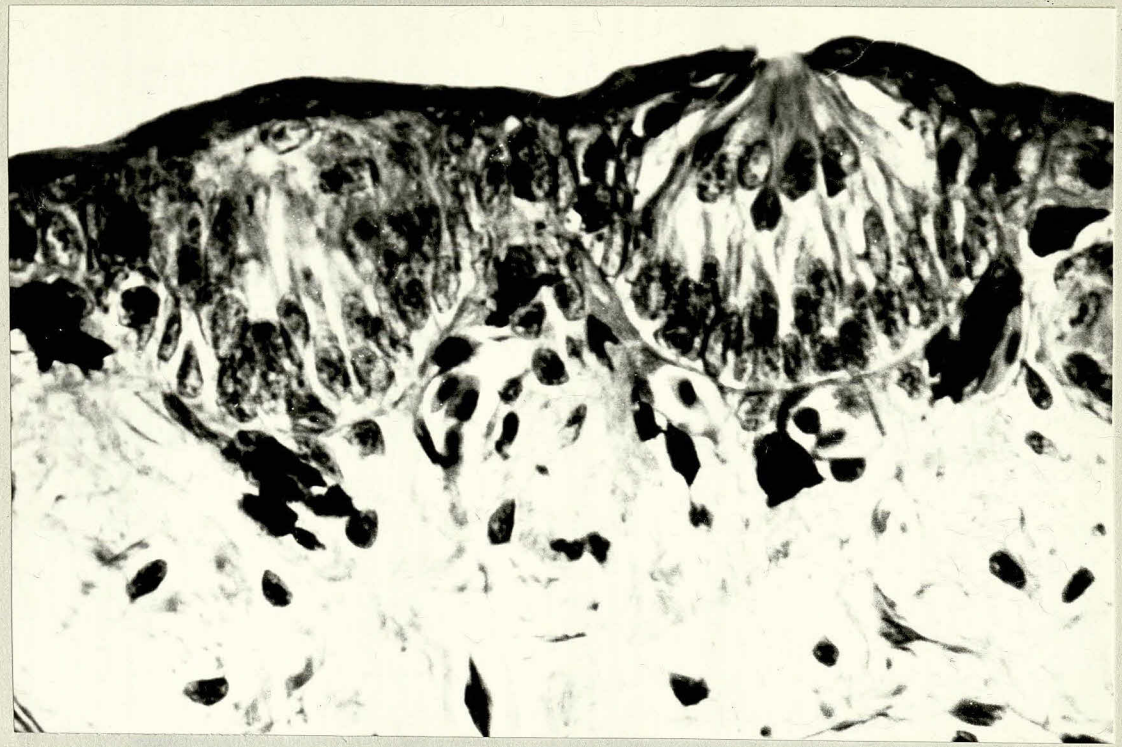


FIG A: Transverse section of two Lateral Line organs (x 400).

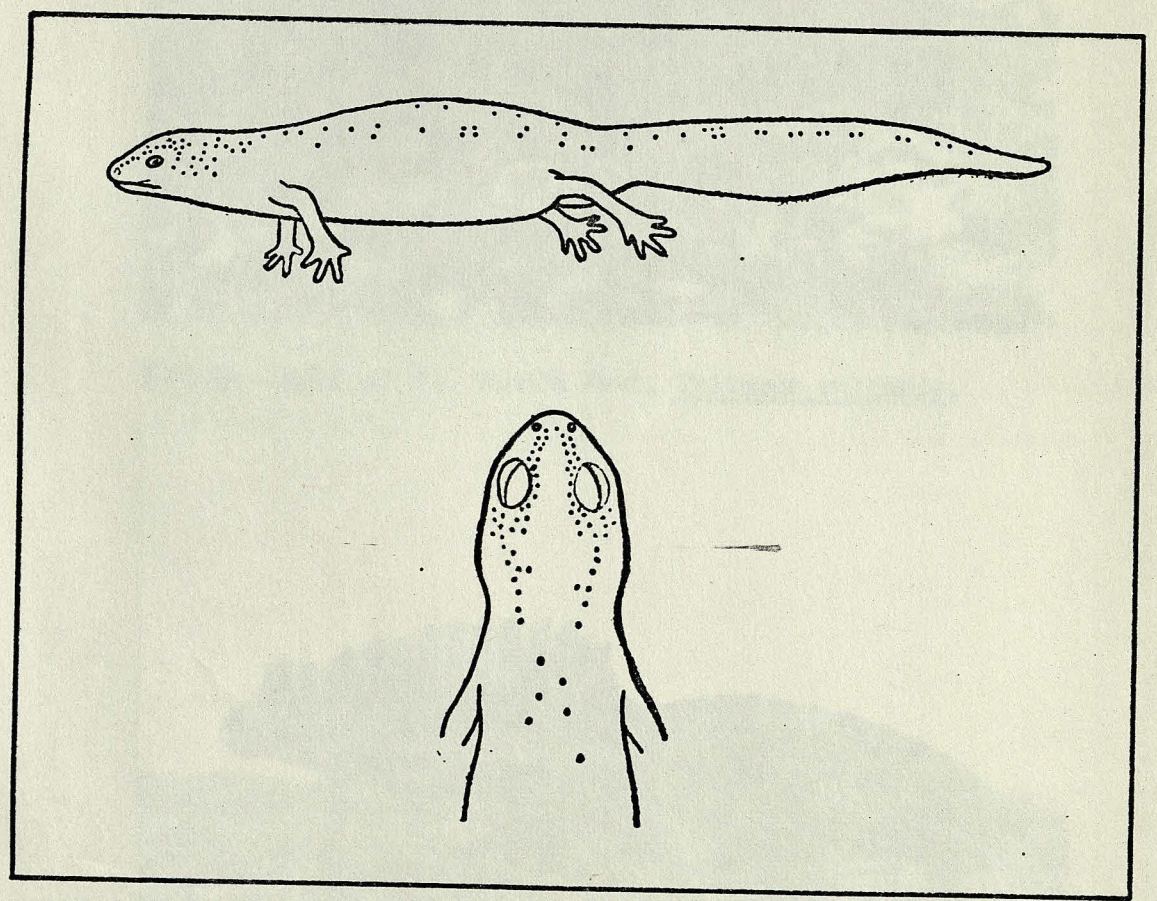


FIG B: Distribution of Lateral Line organs in the Smooth Newt, Triturus vulgaris.

Reproduced from Smith (1951).

LATERAL LINE ORGANS

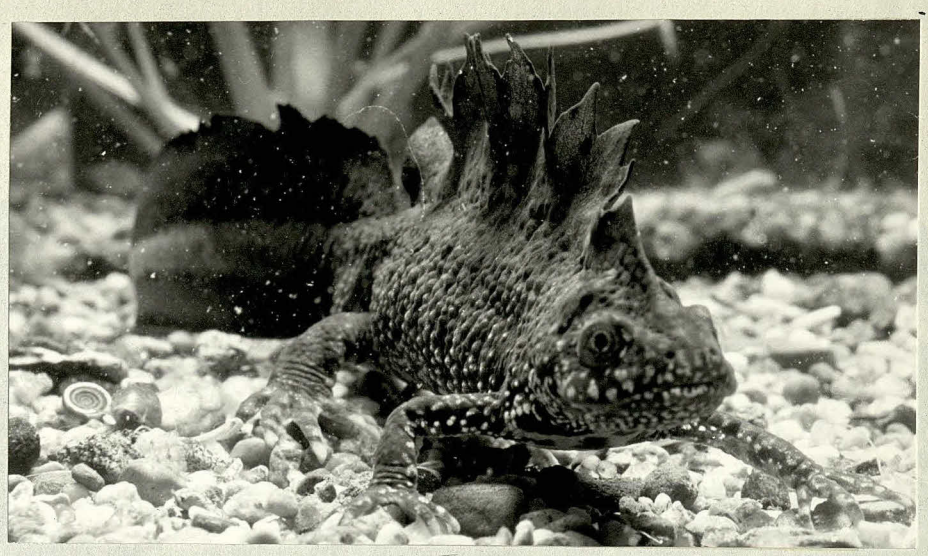


FIG A: Male of the Crested Newt, Triturus cristatus.



FIG B: Male of the Smooth Newt, Triturus vulgaris.

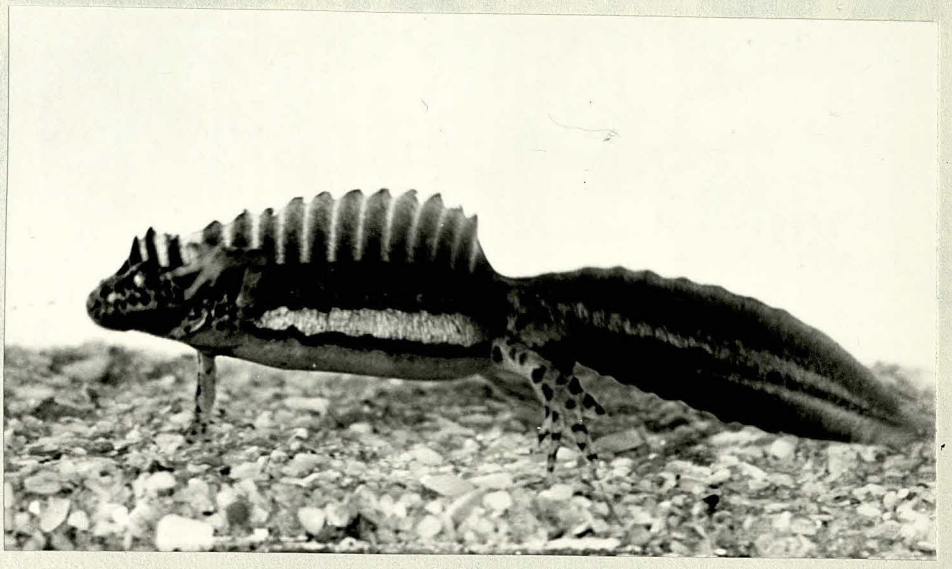


FIG C: Male of the Banded Newt, Triturus vittatus.

DORSAL CRESTS IN MALE NEWTS



FIG A: Transverse section showing a large gland on the left and a smaller gland on the right. The two structures at the top are Lateral Line organs (x 200).

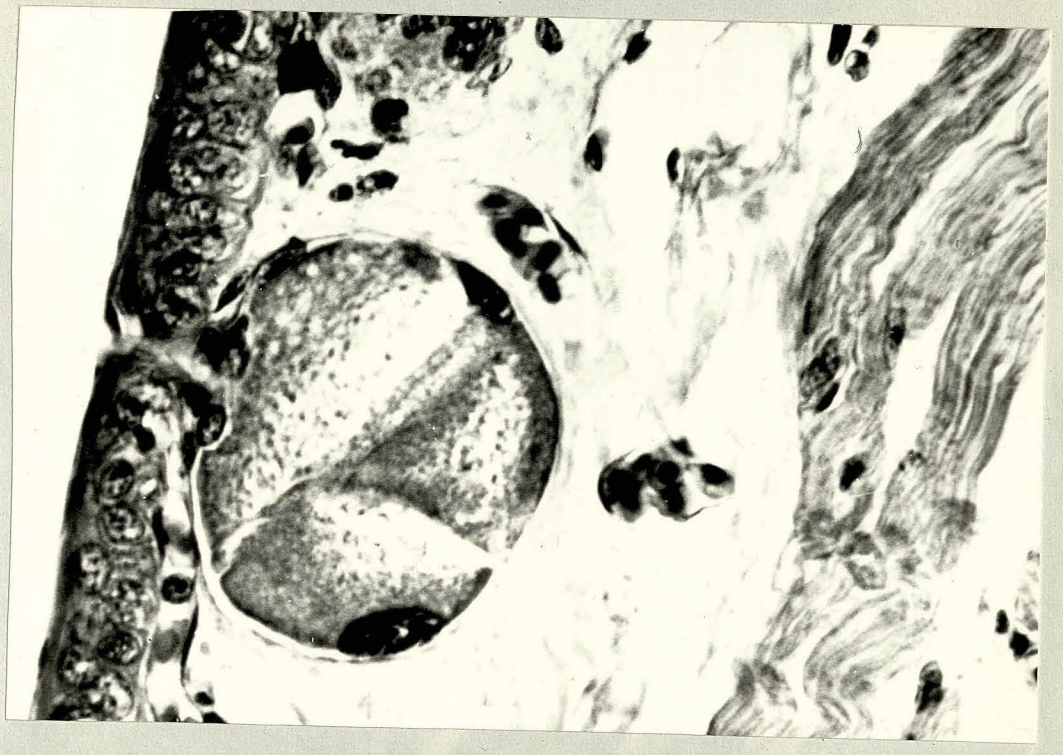


FIG B: Transverse section showing the duct from a gland to the outside world (x 400).

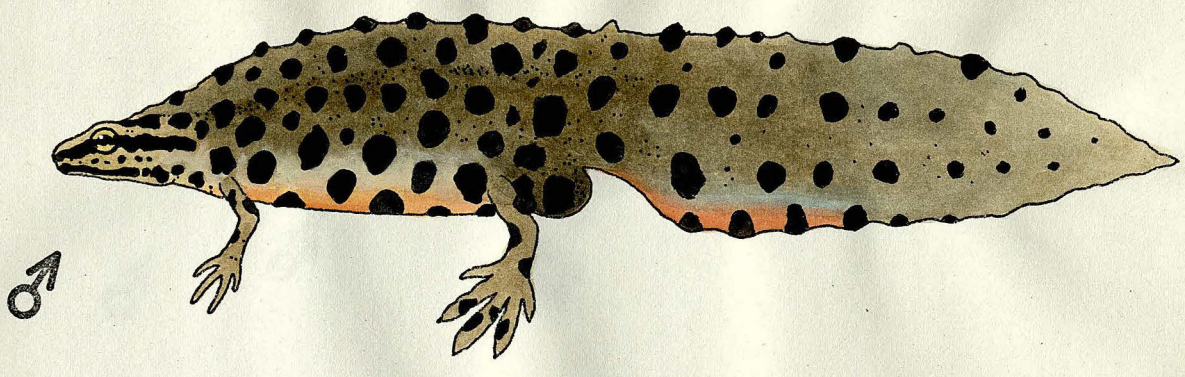
SKIN GLANDS



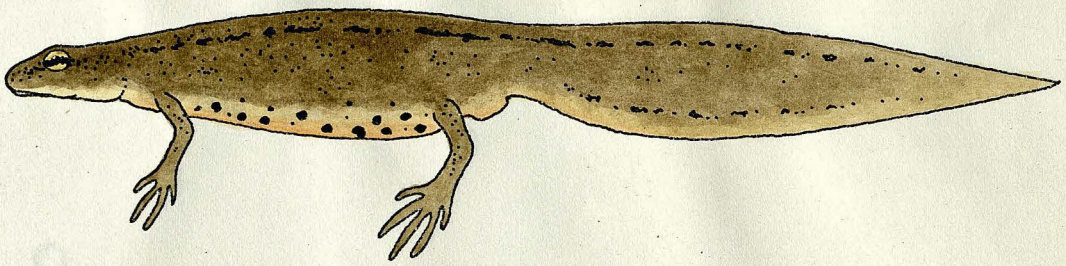


EGG LAYING

Two views of female Smooth Newts, Triturus vulgaris.



♂

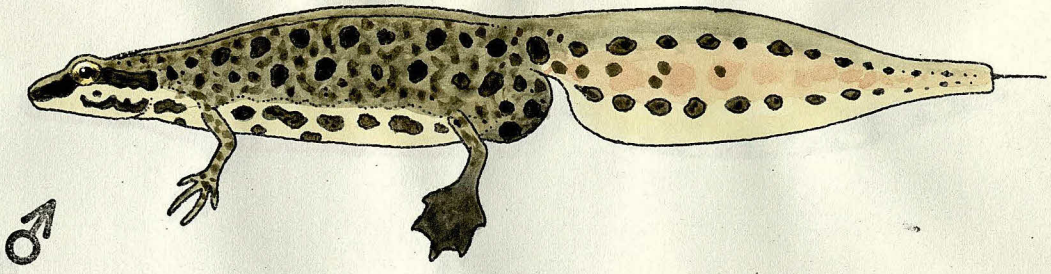


♀

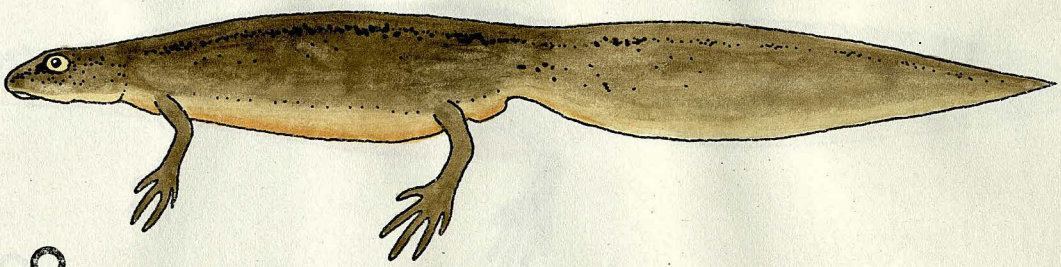
THE SMOOTH NEWT

Triturus vulgaris

x $1\frac{3}{4}$



♂



♀

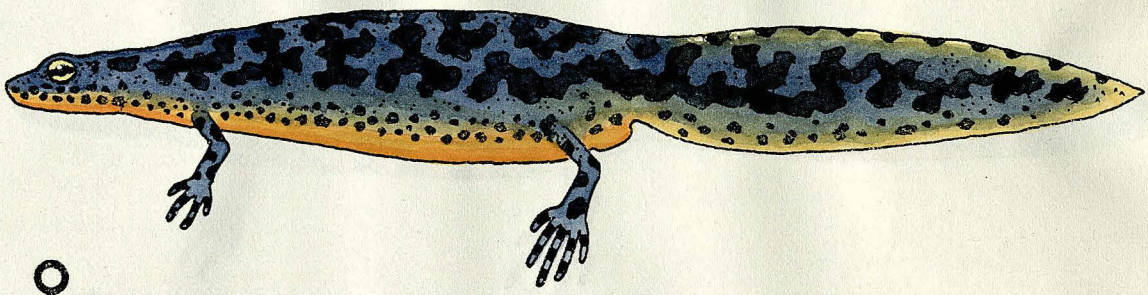
THE PALMATE NEWT

Triturus helveticus

x 2



♂



♀

THE ALPINE NEWT

Triturus alpestris

x $1\frac{3}{4}$



♂



♀

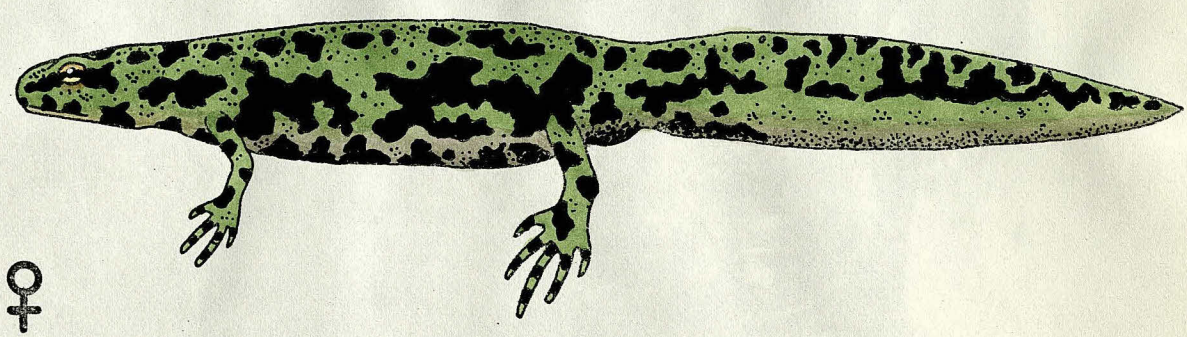
THE CRESTED NEWT

Triturus cristatus

Actual size.



♂



♀

THE MARBLED NEWT

Triturus marmoratus

Actual size.

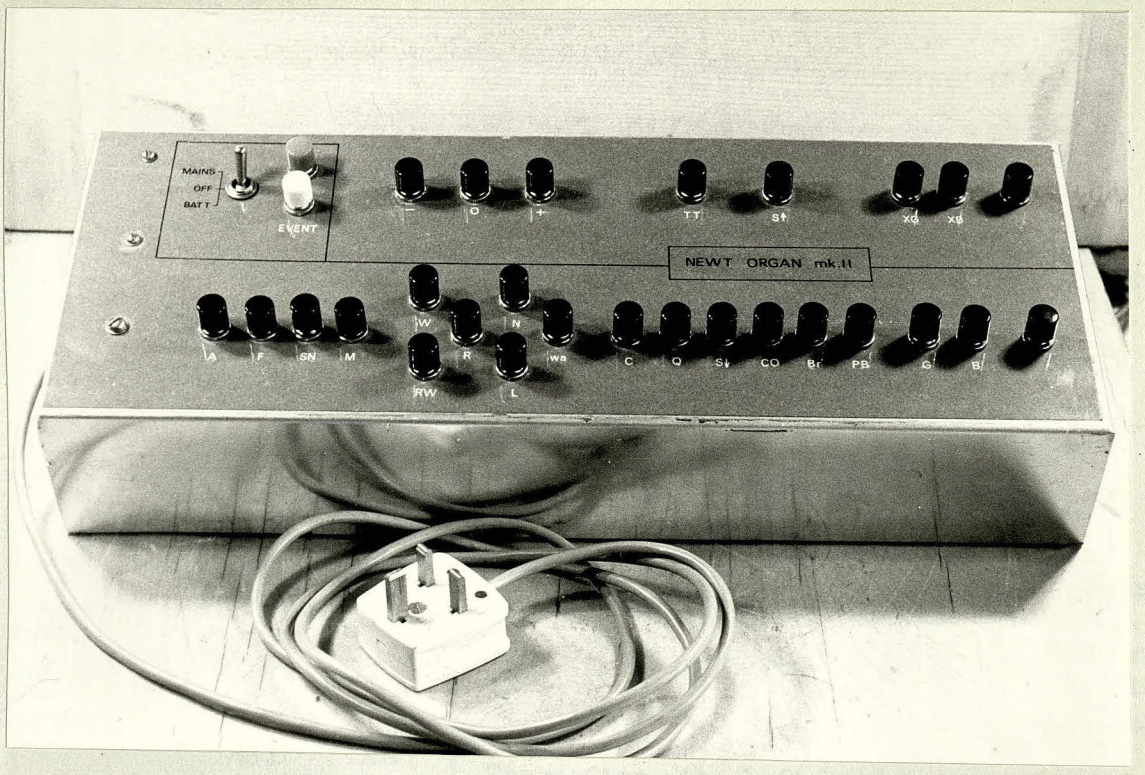


FIG A: Dorsal view showing keyboard.

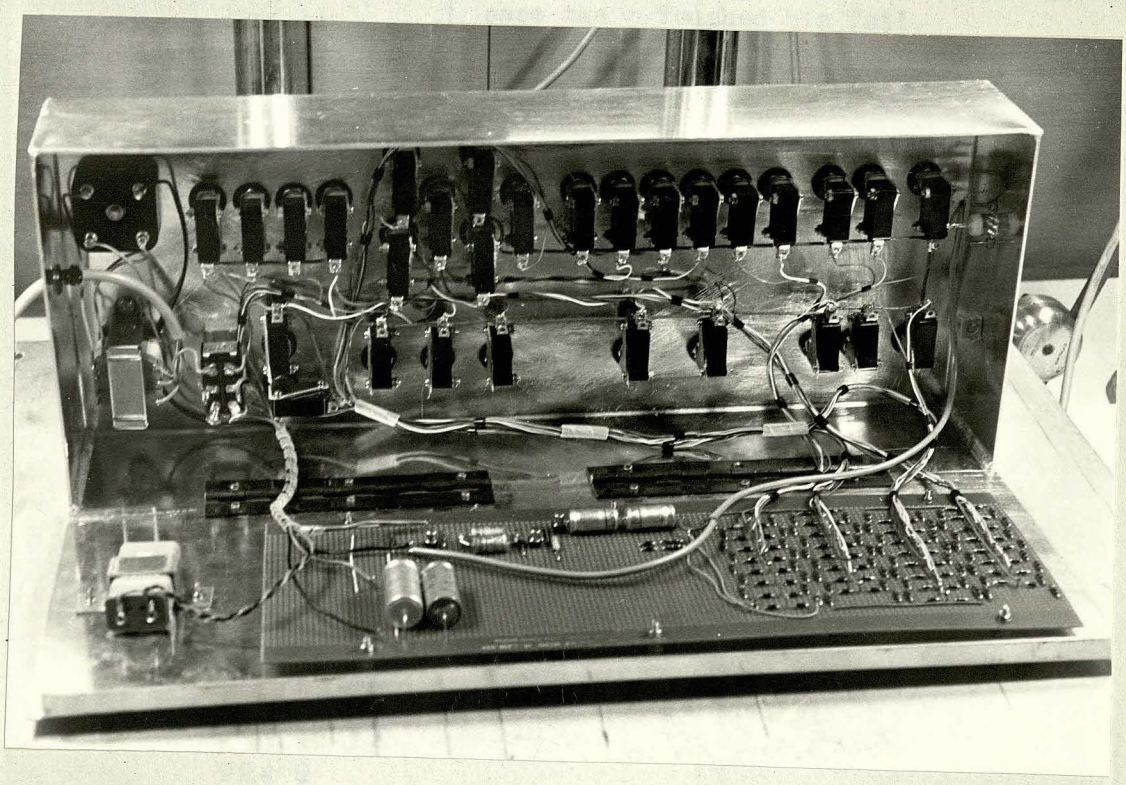


FIG B: Ventral view showing interior circuitry.

THE ORGAN

```
VB 13
19 3 71
M 21   F 08
T  19


  14 A
  51     XA
  62 SN
  79 R
  91 N
 127 N
 258     XA
 282 RW
 291     XA
 314 RW
 351     XX
 373     XA
 427 RW
 434     XA
 473 WA
 482     XA
 497 RW
 504     XA
 526 RW
 533     XA
 560 RN
 566     XA
 571 RN
 577 R
 585     XA
 599 RN
 605     XA
 624 RN
 630 RW
 635     XA
 648 C
 666     XA
 674 Q
 697     TT
 704 S
 737 CO
 750     XA
 768 BR
 796     TT
 848 RW
 855     XA
 876 RW
 884     XA
 909 C
 918     XA
 924 Q
 939     TT
 996 S
1019 CO
1032     XA
1051 BR
1067     TT
1081 PB
1259 RW
1301     XA
1325 RW
1336     XA
1356 RW
```

AN "ORGAN" PRINT-OUT

Part of the record of one courtship encounter.

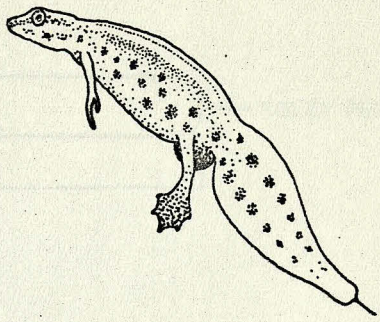
The first 4 lines show a reference number, the date, the identities of the animals involved, and the temperature of the observation tank.

Thereafter, the left-hand column gives the time from the start of observation in tenths of seconds, the middle column shows ♂ acts and the right-hand column shows ♀ acts.

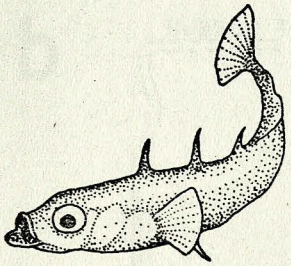
Thus - at 67.4 secs the ♂ Quivered and at 69.7 secs the ♀ Touched his Tail.



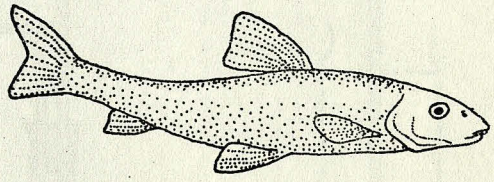
♂ Smooth Newt



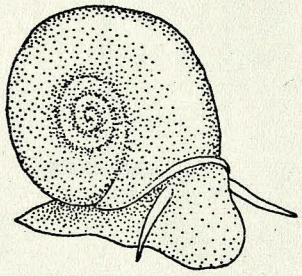
♂ Palmate Newt



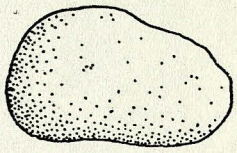
Stickleback



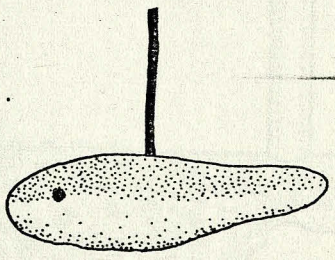
Gudgeon



Snail

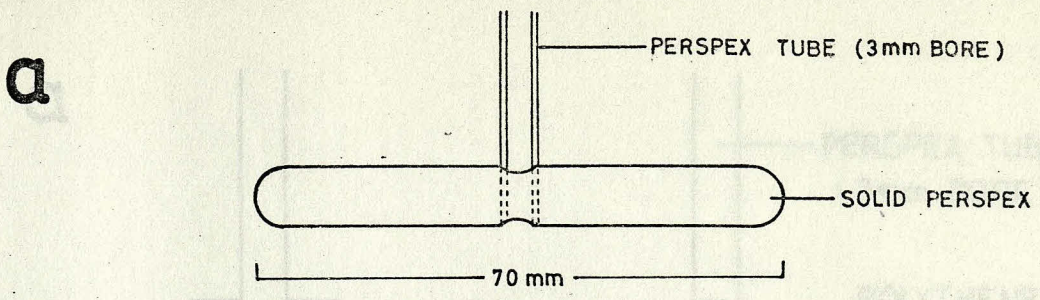


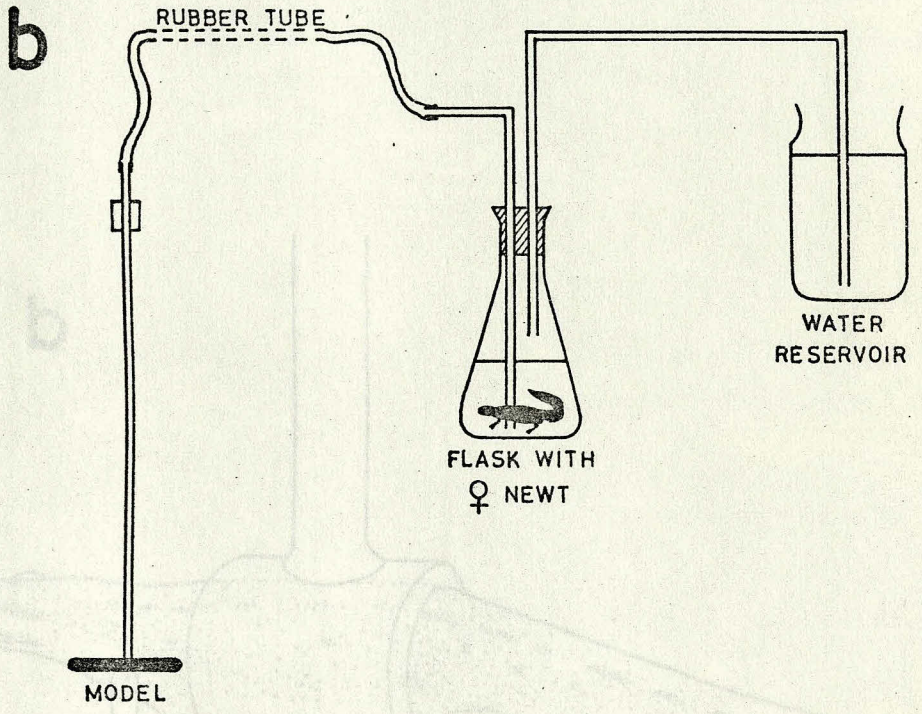
Stone

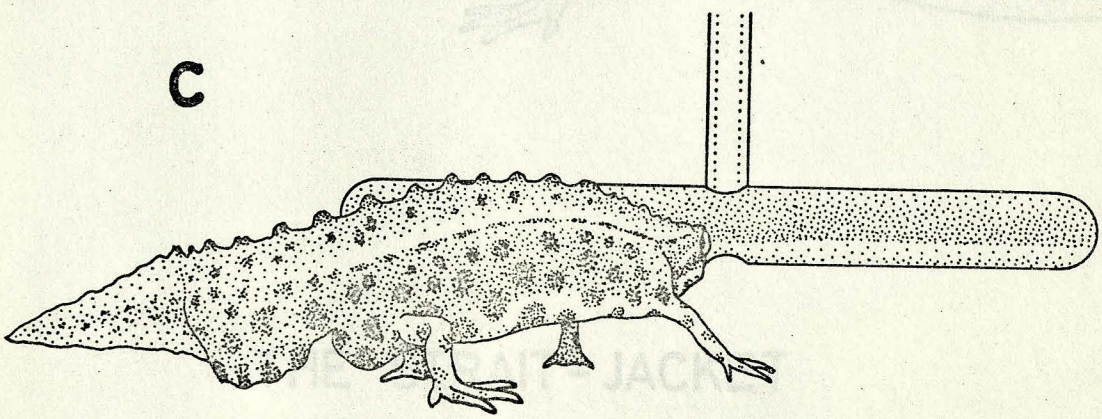


Stickleback dummy

OBJECTS DISPLAYED TO BY MALE SMOOTH NEWTS *T. vulgaris*

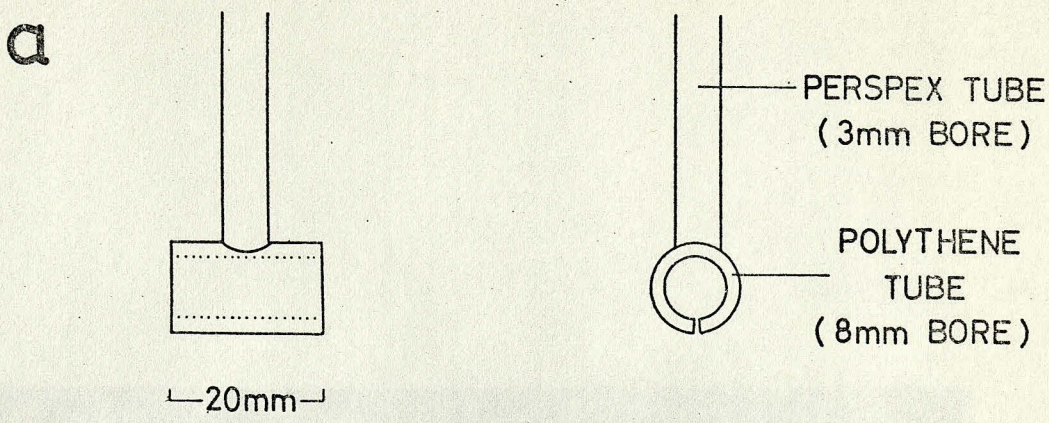


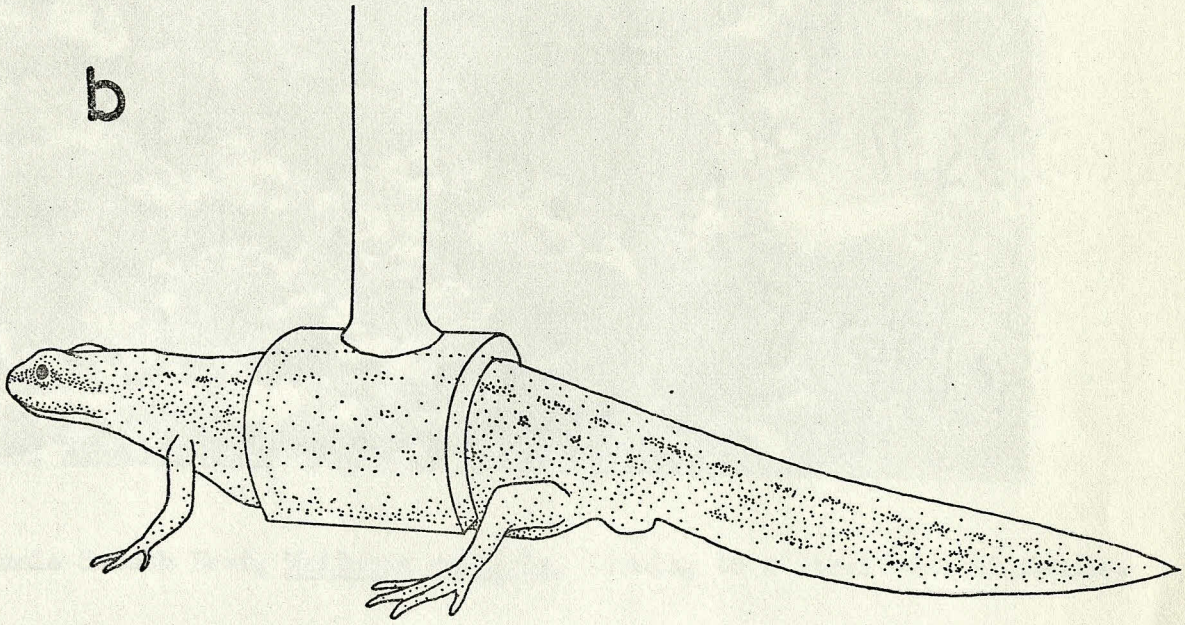




♀ NEWT MODEL

a: The model.
b: The system for syphoning ♀ smell through the model.
c: A T. vulgaris ♂ sniffing a ♀ model.





THE STRAIT-JACKET

a: Side and End views of Strait - Jacket.
b: A T. vulgaris ♀ in a Strait - Jacket.



A male Smooth Newt, Triturus vulgaris, Fanning to a Strait-Jacket female.

THE STRAIT-JACKET



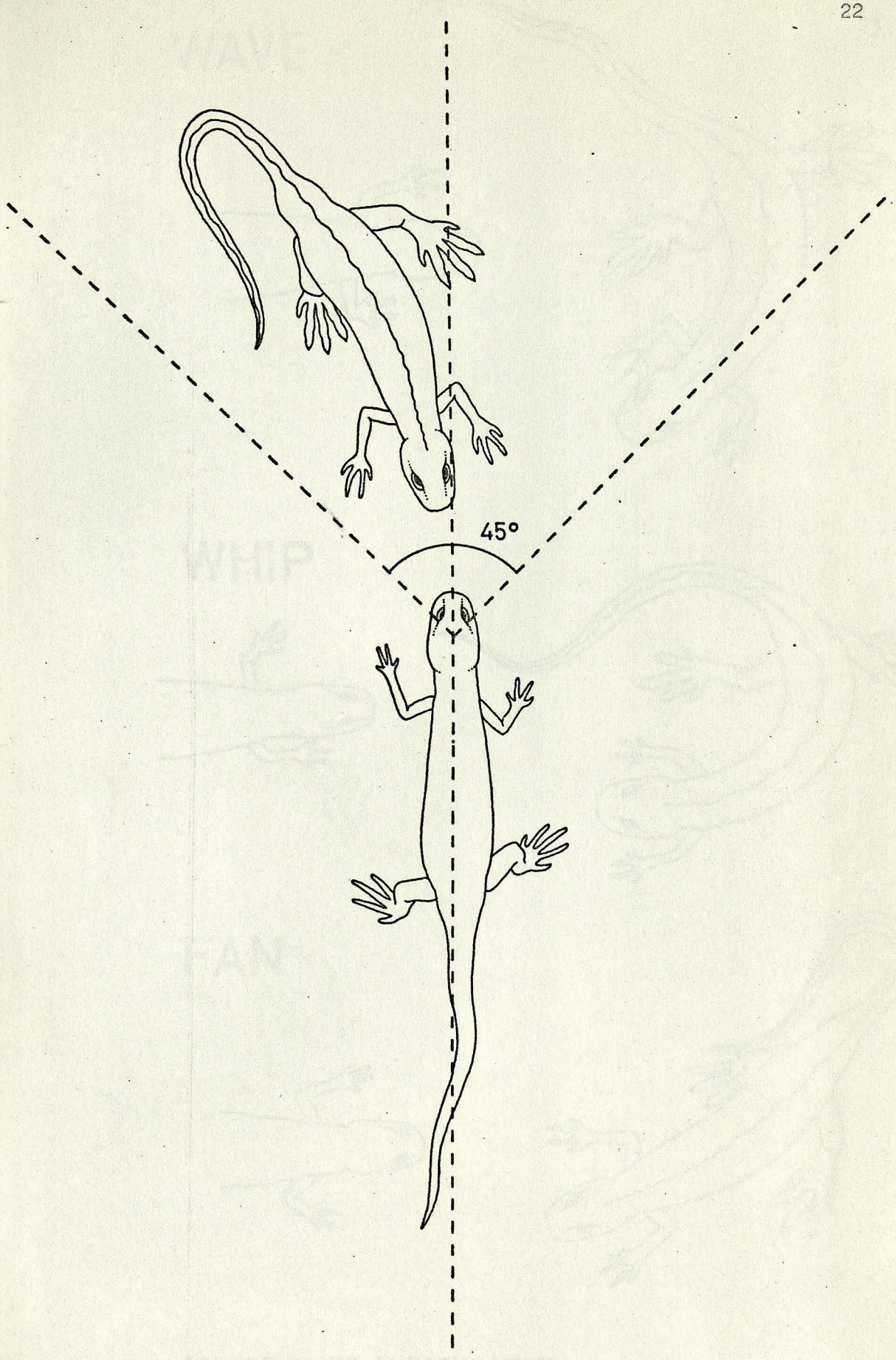
FIG A: A male in the Alert Posture.



FIG B: A male Moving-to-the-Front of a female.

COURTSHIP OF SMOOTH NEWT:

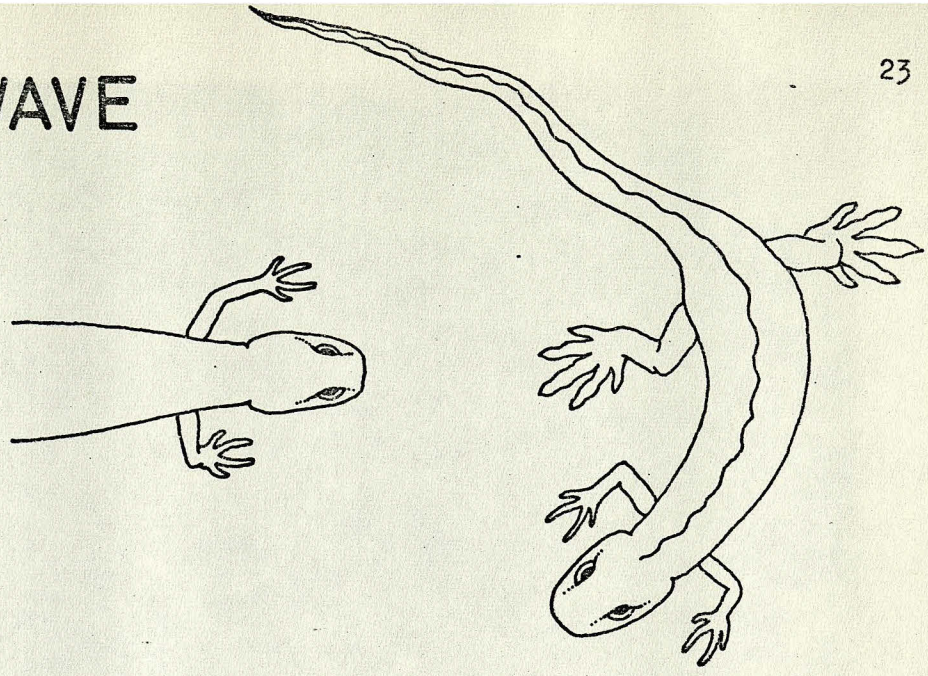
ALERT POSTURE AND MOVE-TO-THE-FRONT.



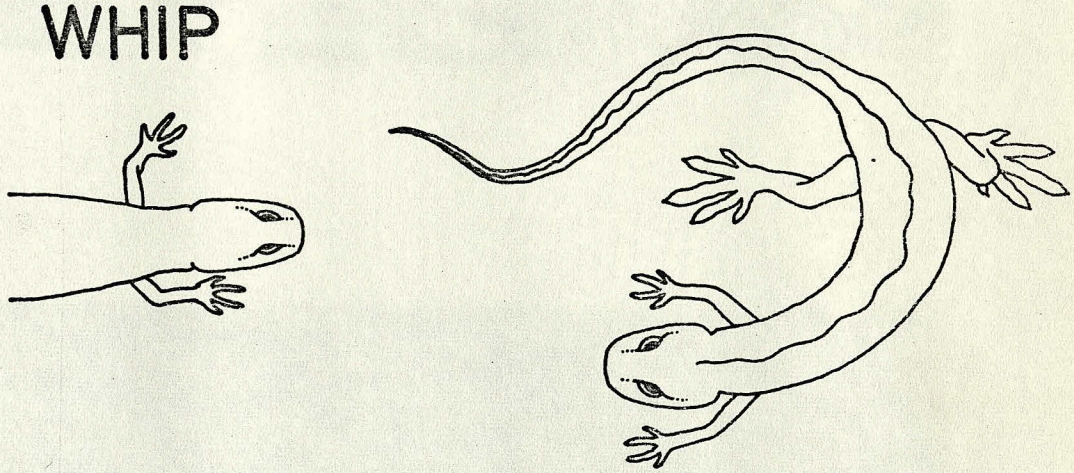
COURTSHIP OF SMOOTH NEWT

THE ♂'s DISPLAY ORIENTATION

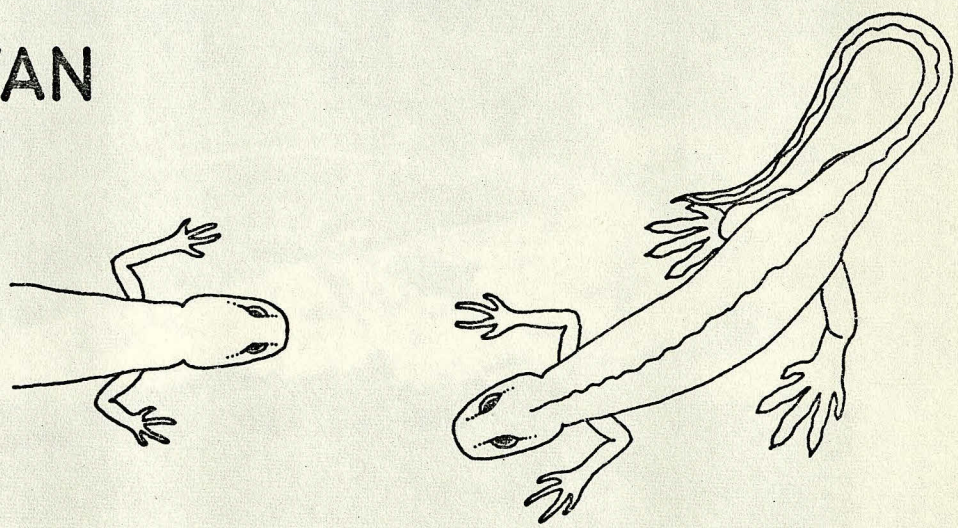
WAVE



WHIP



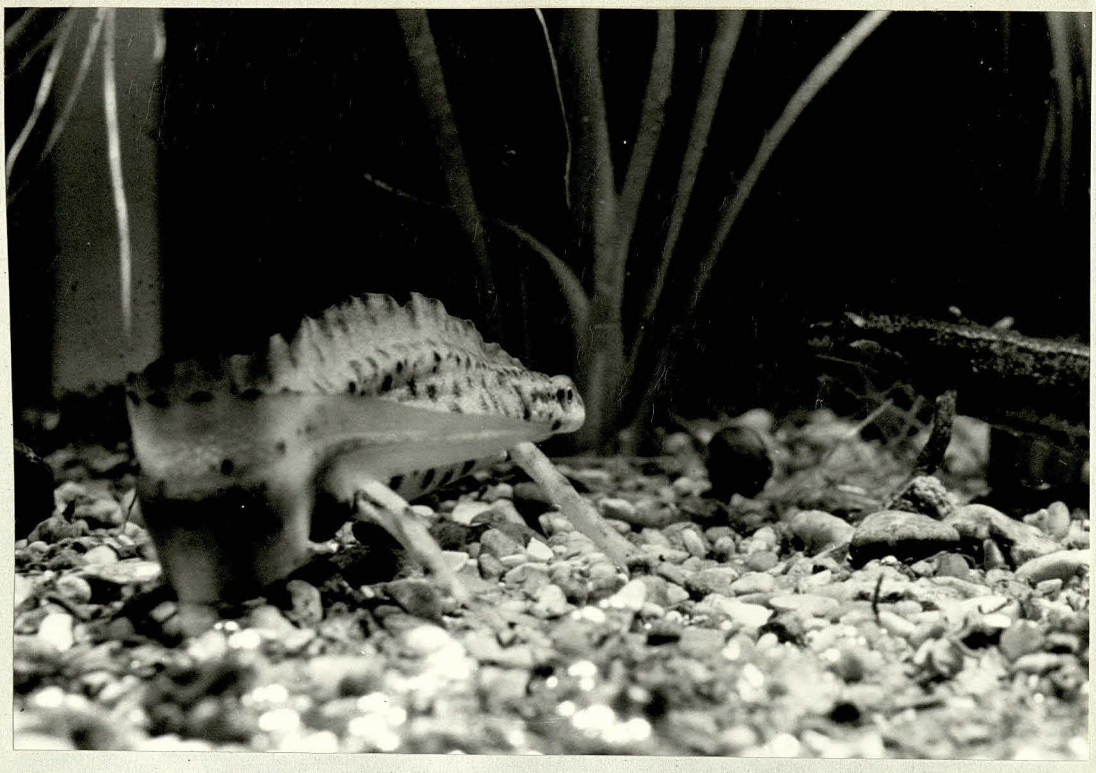
FAN



COURTSHIP OF SMOOTH NEWT:

THE ♂'s DISPLAY MOVEMENTS

The male is on the right.





COURTSHIP OF SMOOTH NEWT:

FANNING

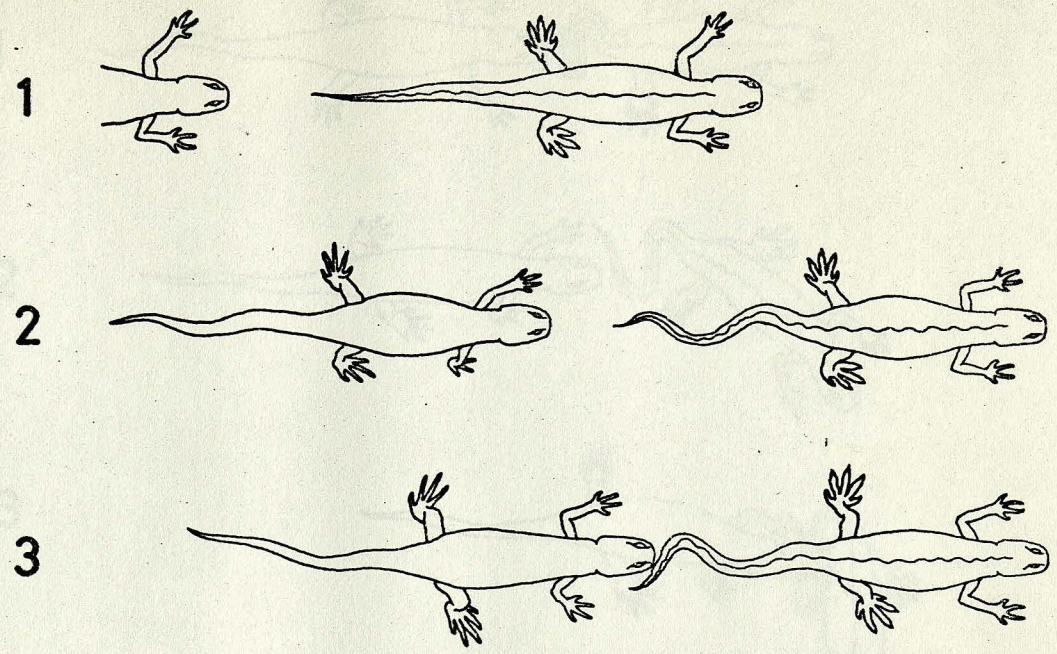




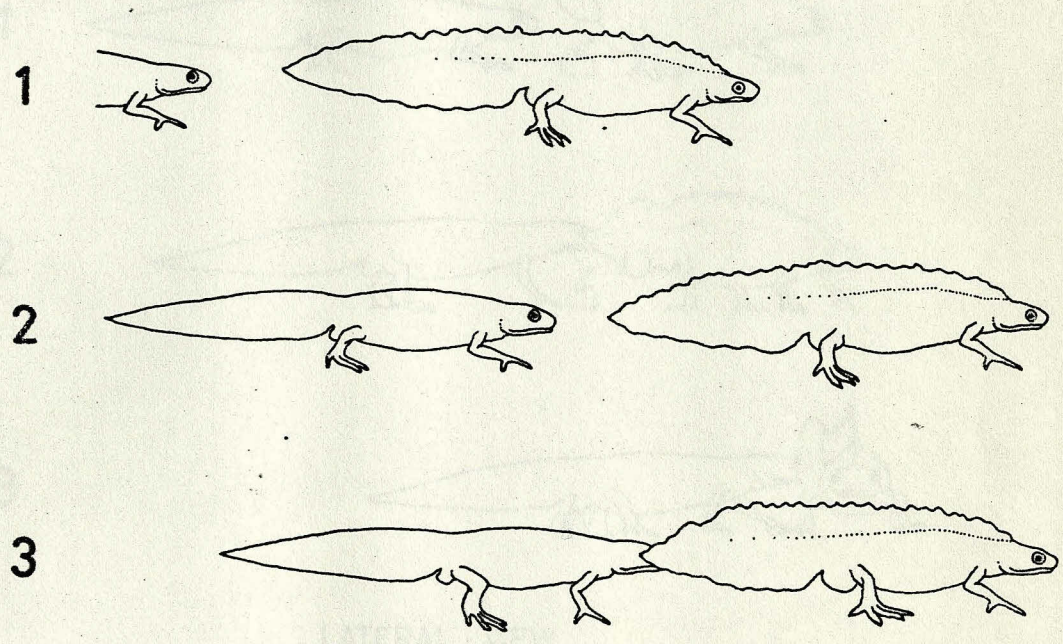


COURTSHIP OF SMOOTH NEWT:

THE WAVE



DORSAL VIEW



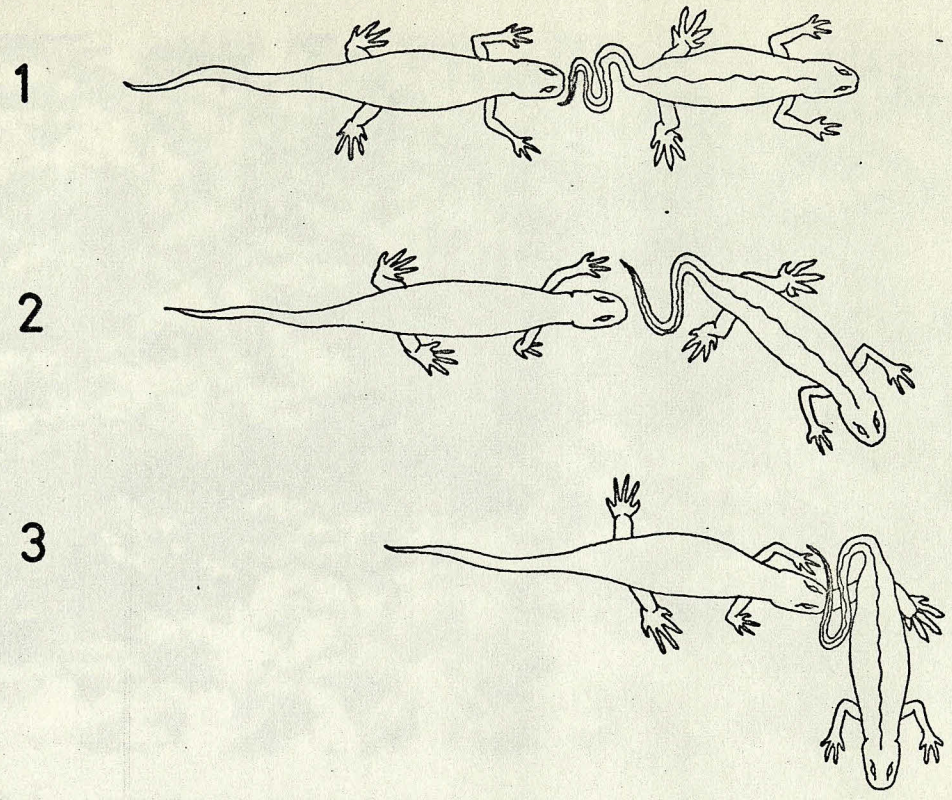
LATERAL VIEW

COURTSHIP OF SMOOTH NEWT:

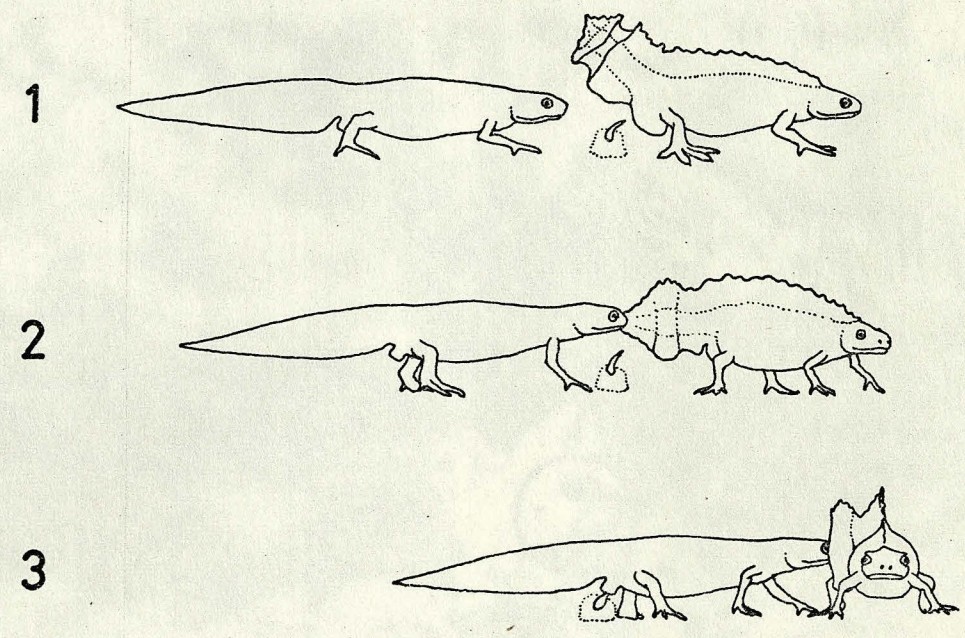
DEPOSITION PHASE 1.

1: CREEP. 2: QUIVER. 3: TOUCH - TAIL.

The male is on the right.



DORSAL VIEW



LATERAL VIEW

COURTSHIP OF SMOOTH NEWT:

DEPOSITION PHASE 2.

1: DEPOSITION. 2: CREEP-ON. 3: BRAKE.

The male is on the right.



FIG A: QUIVER and TOUCH-TAIL.



FIG B: Deposition of the Spermatophore (ringed).

COURTSHIP OF SMOOTH NEWT:

DEPOSITION PHASE 1.



FIG A: Male beginning to CREEP-ON.

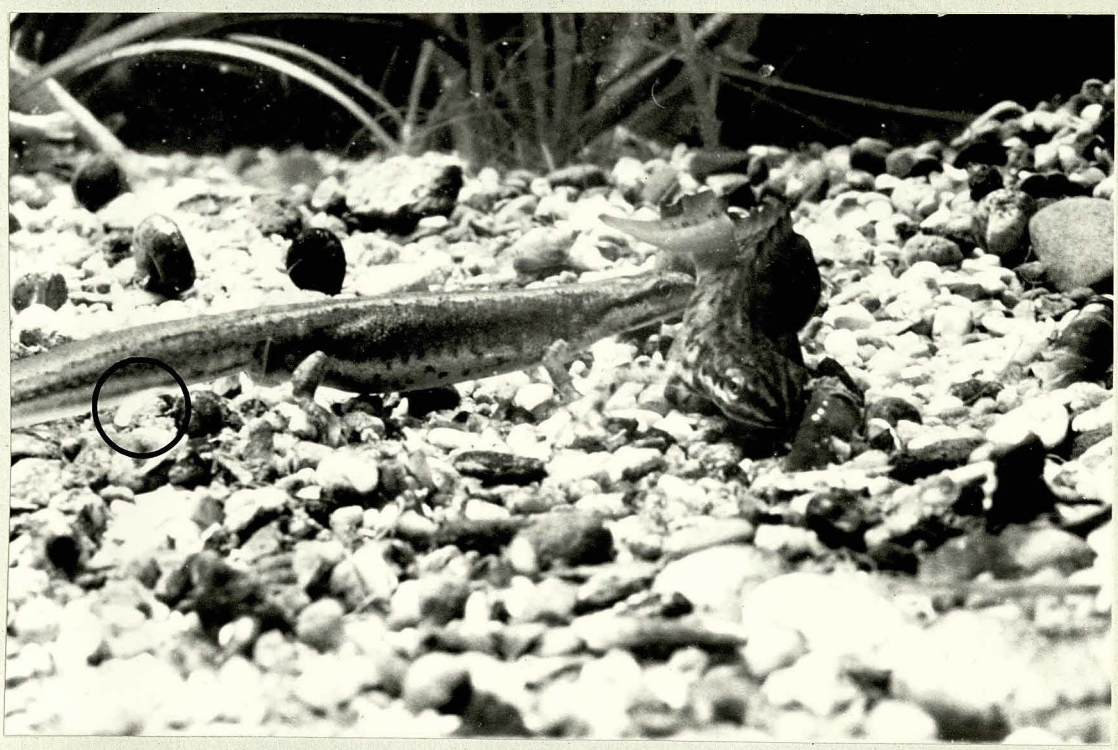
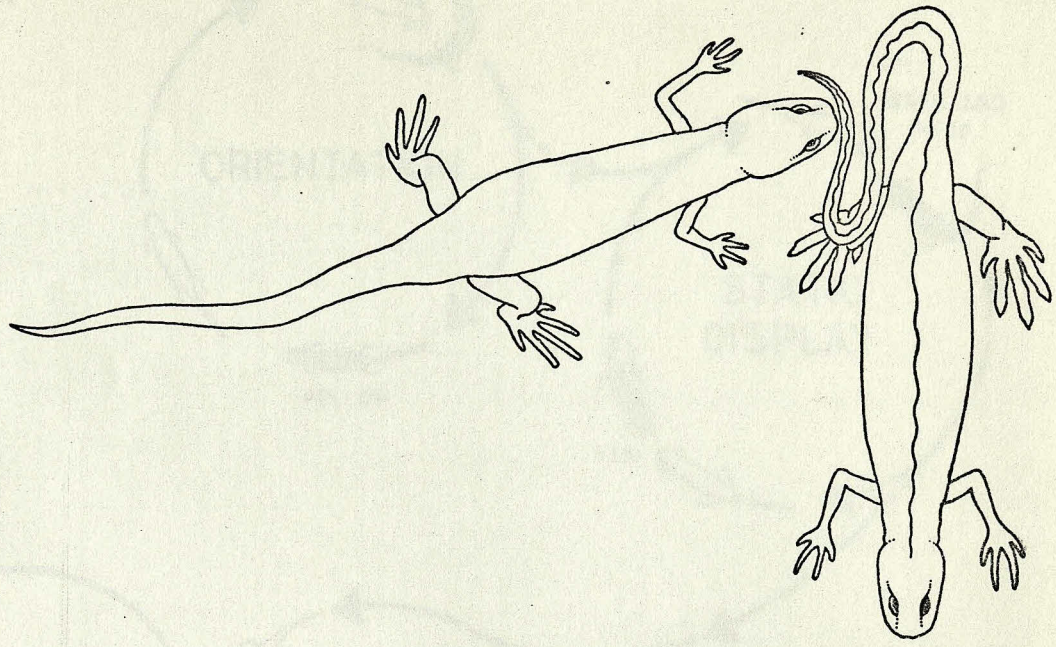


FIG B: BRAKING. Note that the Spermatophore (ringed) has been missed.

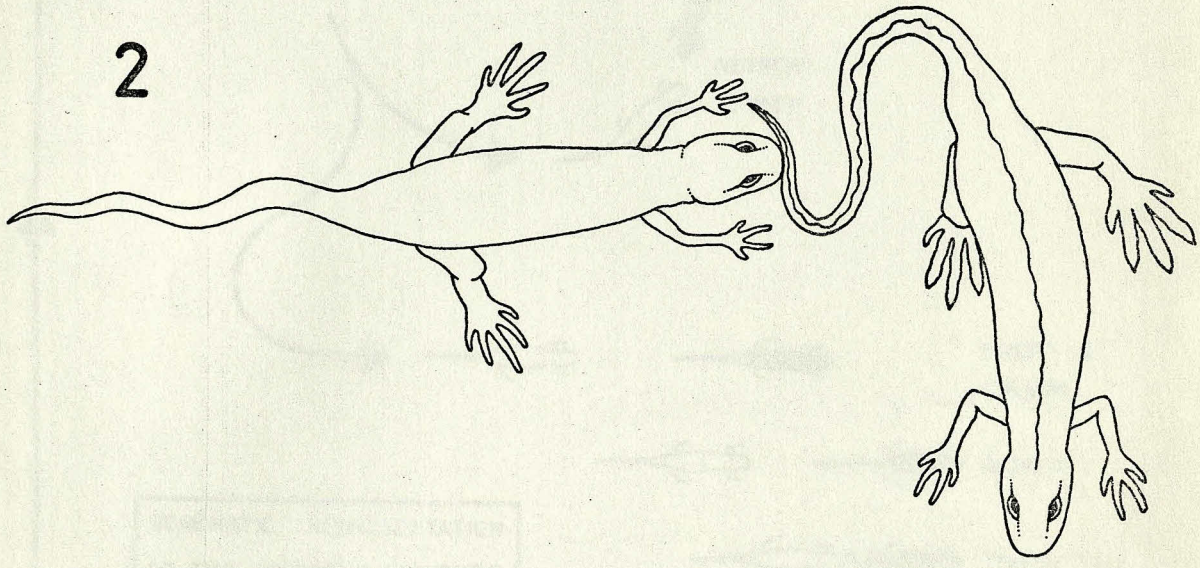
COURTSHIP OF SMOOTH NEWT:

DEPOSITION PHASE 2.

1



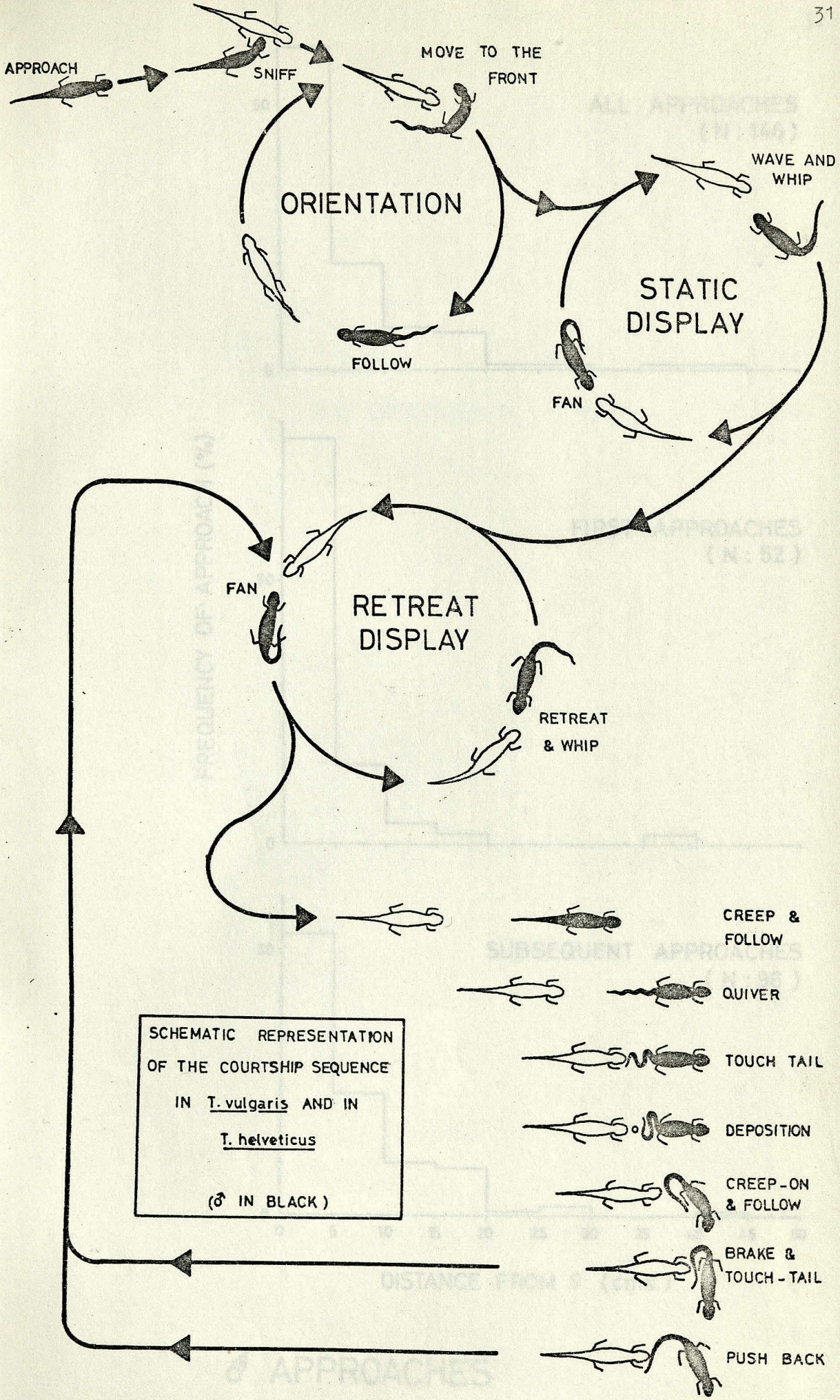
2



COURTSHIP OF SMOOTH NEWT

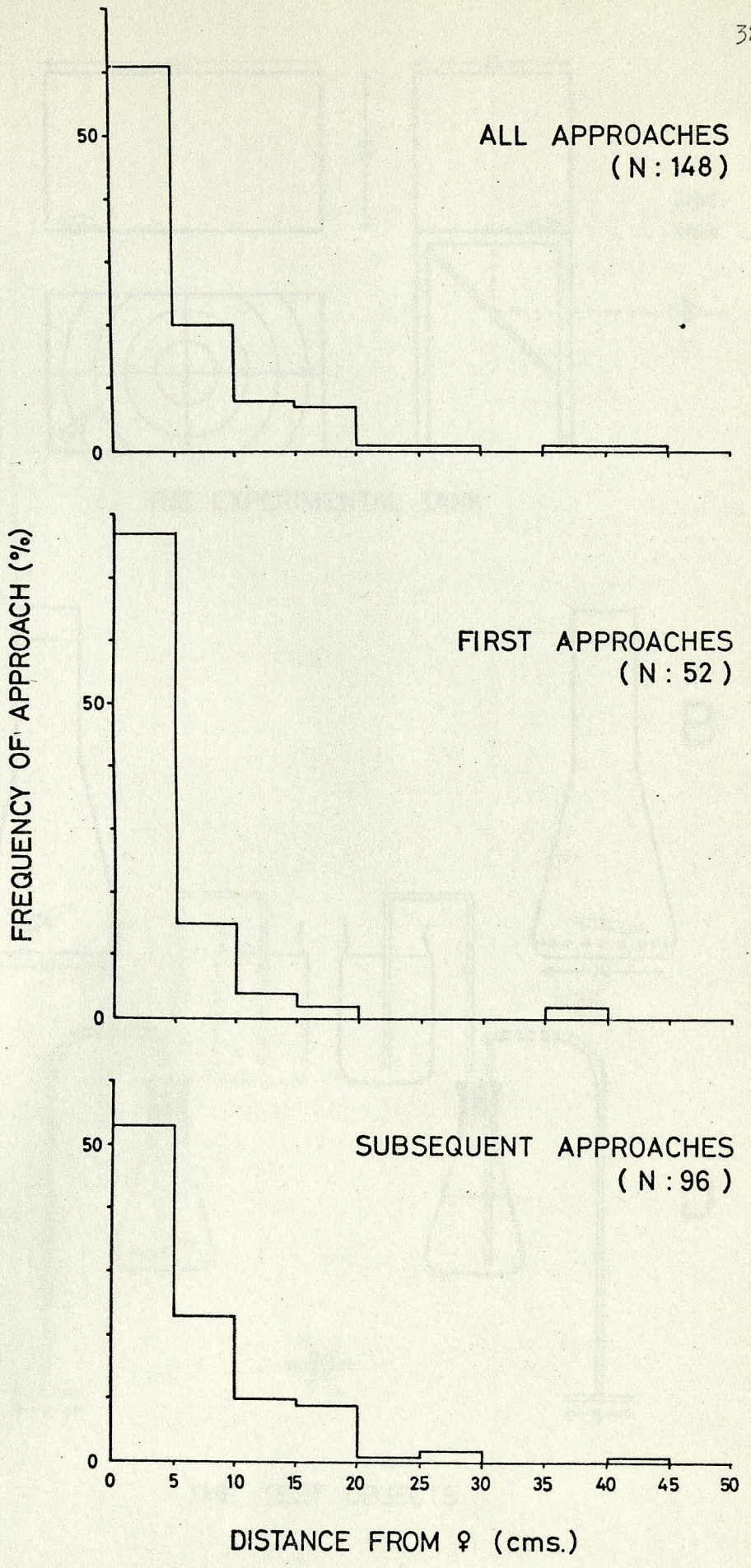
PUSH BACK

The male is on the right.



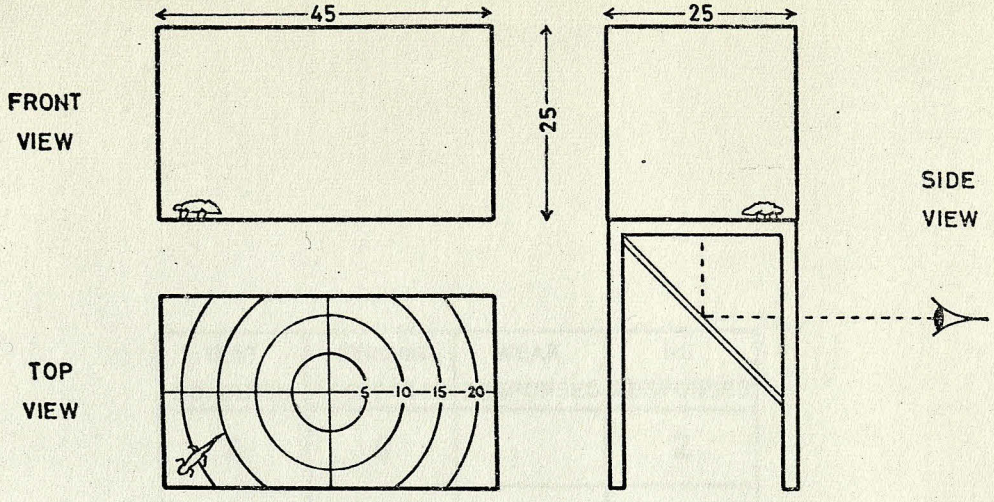
SCHEMATIC REPRESENTATION OF THE COURTSHIP SEQUENCE IN T. vulgaris AND IN T. helveticus

(♂ IN BLACK)

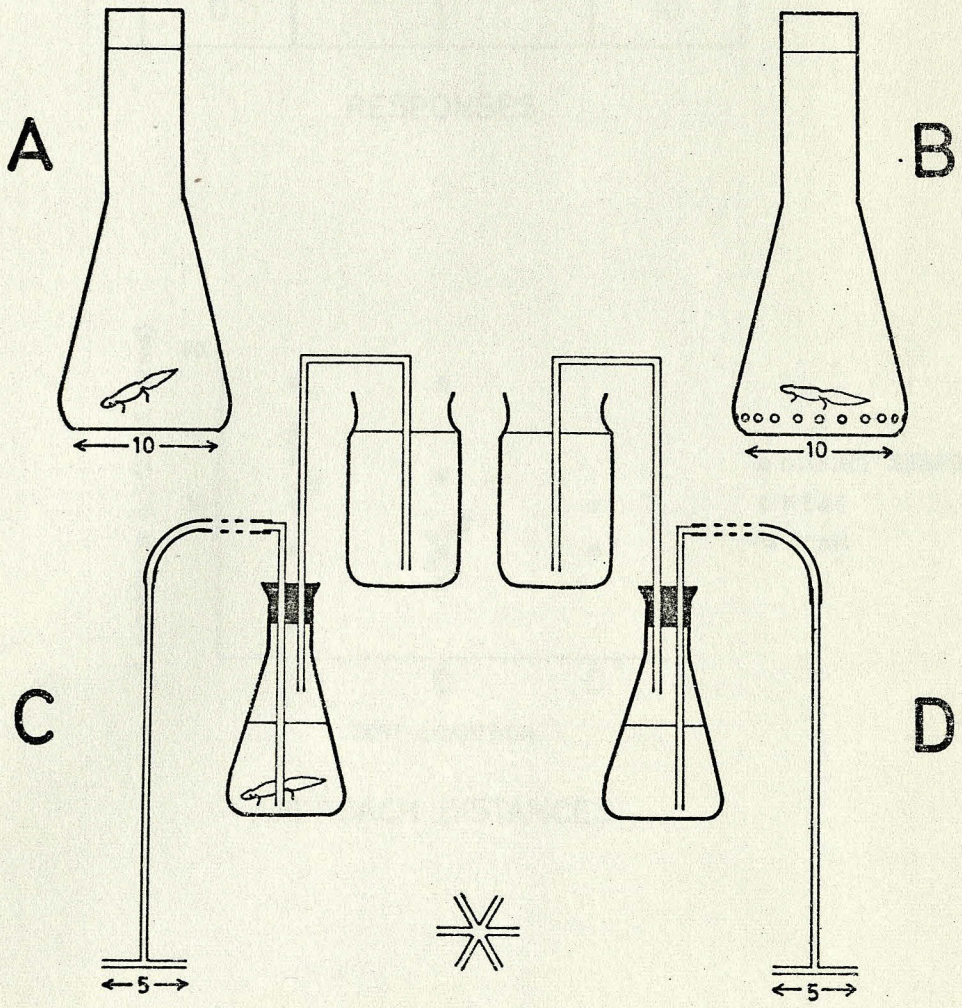


♂ APPROACHES

For raw data see Appendix 3 a.



THE EXPERIMENTAL TANK



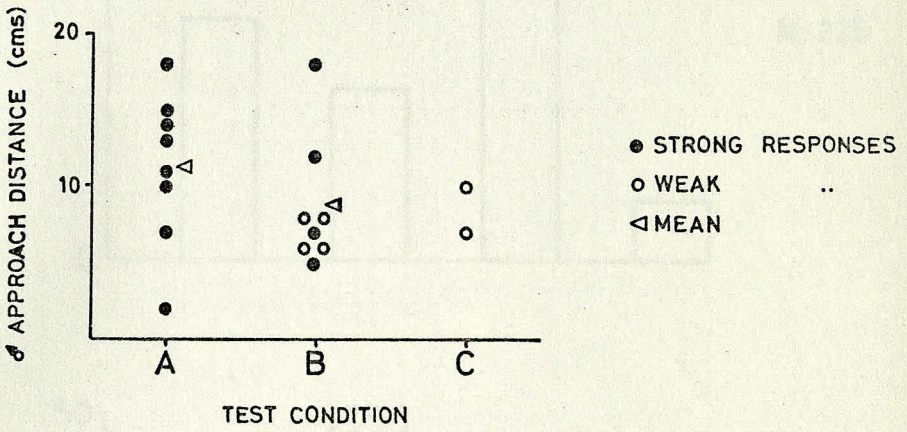
THE TEST OBJECTS

THE ♂ APPROACH EXPERIMENT

All dimensions in cm.

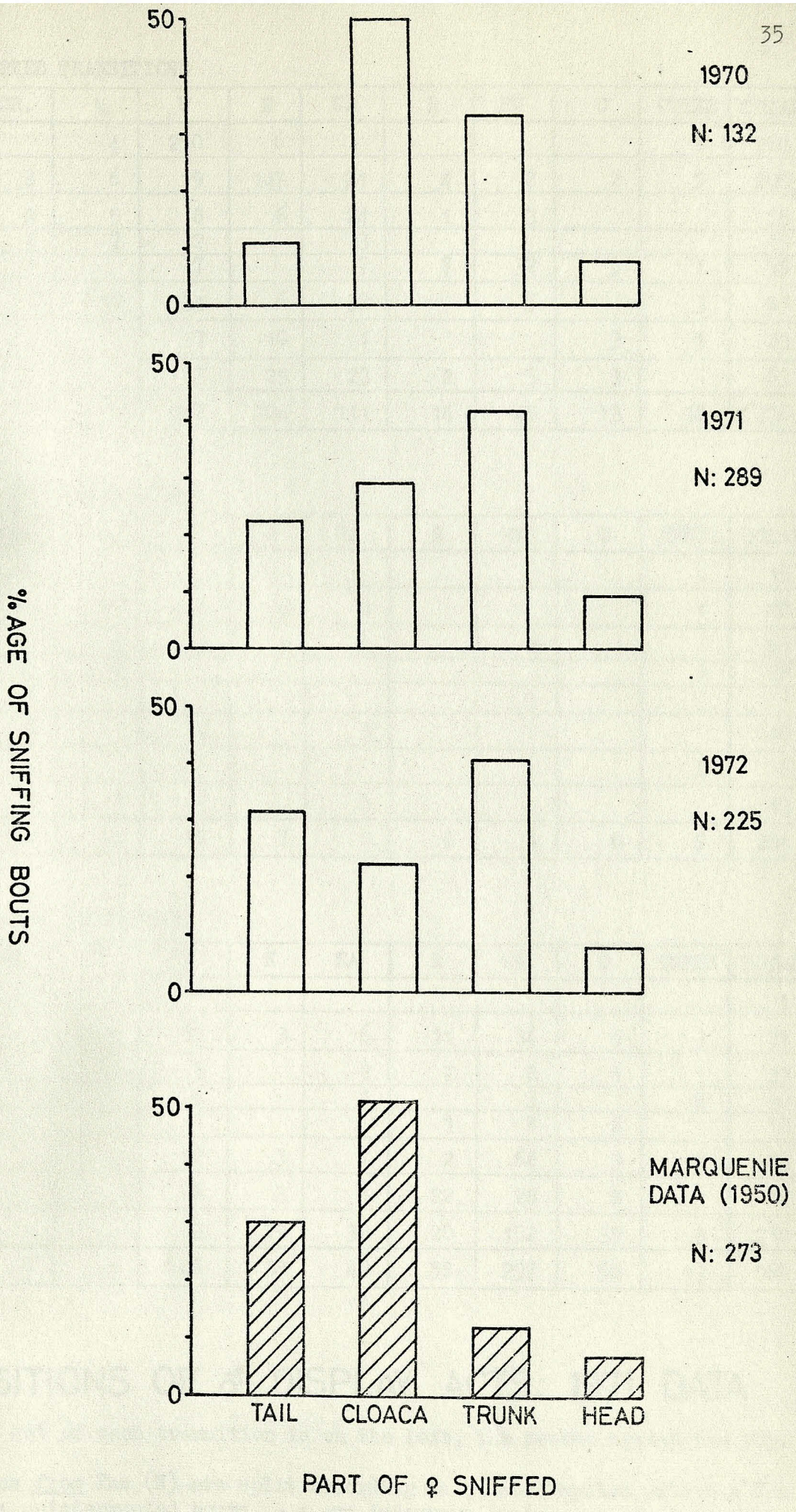
TEST CONDITION	STRONG RESPONSES	WEAK RESPONSES	NO RESPONSES
A	8		2
B	4	4	2
C		2	8
D			10

RESPONSES



APPROACH DISTANCES

THE ♂ APPROACH EXPERIMENT RESULTS



DISTRIBUTION OF ♂ SNIFFING BOUTS

For raw data see Appendix 3 c.

UNINTERRUPTED TRANSITIONS

		OR.	M	W	N	WA	R	RW	C	OTHER	TOTAL
M			4	250	6					2	262
W		2	6	19	147	21	4	2	2	5	208
N	U	8	5	8	6	24	1	3			55
	-	7	7	2		3					19
	+			7		7	7	32	5	1	59
WA			10	31	6	32		5		3	87
R		1		7	10	1			3	1	23
RW				3	29	23	2	3	3		63
TOTAL		18	32	327	204	111	14	45	13	12	776

-VE INTERRUPT TRANSITIONS

		OR.	M	W	N	WA	R	RW	C	OTHER	TOTAL
M		14								1	15
W		53	15	5	5	1				1	80
N	U	42	4	1	2	1		1			51
	-	25	2							1	28
	+	1									1
WA		5		2		3					10
R		4								2	6
RW		7	1	2		3					13
TOTAL		151	22	10	7	8	0	1	0	5	204

+VE INTERRUPT TRANSITIONS

		OR.	M	W	N	WA	R	RW	C	OTHER	TOTAL
M			1								1
W				15	3	6	11	34	5	3	77
N	U			9		2	2	8	1	1	23
	-			4		1		3		2	10
	+			1			1	8	2		12
WA				12	3	7	2	64	3	2	93
R				2	3	1	22	28	8	2	66
RW				3	29	32	20	152	39	3	278
TOTAL		0	1	46	38	49	58	297	58	13	560

TRANSITIONS OF ♂ DISPLAY ACTS: 1971 DATA

The first act of each transition is on the left, the second across the top.

Transitions <u>from</u> Fan (N) are split according to ♀ interruption within a Fan bout - U : uninterrupted bouts, - : -ve interrupt bouts, + : +ve interrupt bouts.

For full explanation see text.

UNINTERRUPTED TRANSITIONS

		OR.	M	W	N	WA	R	RW	C	OTHER	TOTAL
M			2	226	7					2	237
W		2	11	12	159	24	2		9	3	222
N	U	5	3		18	41		2		1	70
	-	13	6		2	4				2	27
	+		1	1	4	7		21	2	1	37
WA		1	3	87	14	37	2	7			151
R			2	1	5	2			1	7	18
RW			3	5	11	22	2	4	6	1	54
TOTAL		21	31	332	220	137	6	34	18	17	816

-VE INTERRUPT TRANSITIONS

		OR.	M	W	N	WA	R	RW	C	OTHER	TOTAL
M		5									5
W		52	4	1	4	5				2	68
N	U	26	1		1	3				2	33
	-	22								1	23
	+	2									2
WA		8	2	2		3		1		1	17
R		1									1
RW		1	1			1					3
TOTAL		117	8	3	5	12	0	1	0	6	152

+VE INTERRUPT TRANSITIONS

		OR.	M	W	N	WA	R	RW	C	OTHER	TOTAL
M				1	1			1		1	4
W			1	3	2	3	4	14	2	1	30
N	U	1		5	4	8	1	7		2	28
	-			1		2				1	4
	+							5		1	6
WA				3		1	3	47	4	1	59
R				1	1	1	16	48	8	1	76
RW				3	5	17	44	154	62	5	290
TOTAL		1	1	17	13	32	68	276	76	13	497

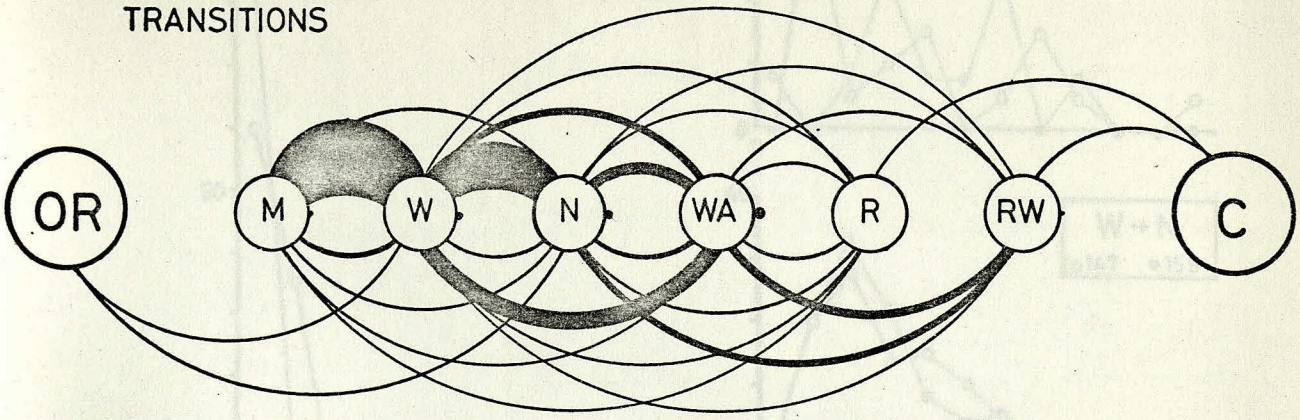
TRANSITIONS OF ♂ DISPLAY ACTS: 1972 DATA

The first act of each transition is on the left, the second across the top.

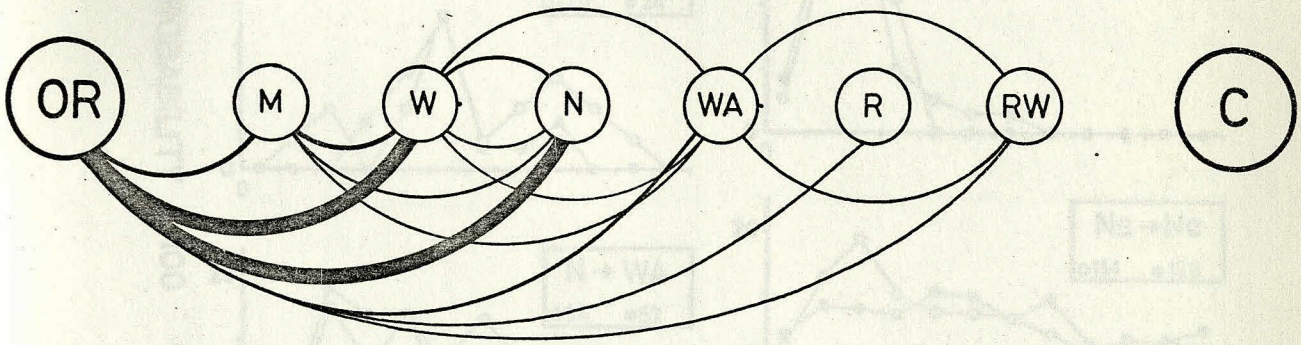
Transitions <u>from</u> Fan (N) are split according to ♀ interruption within a Fan bout - U : uninterrupted bouts, - : -ve interrupt bouts, + : +ve interrupt bouts.

For full explanation see text.

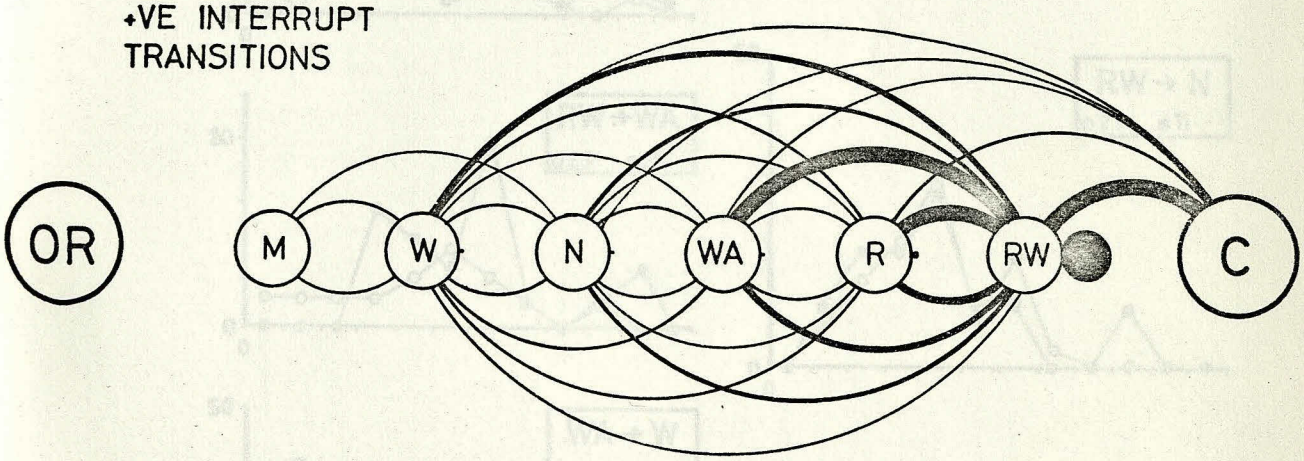
UNINTERRUPTED TRANSITIONS



-VE INTERRUPT TRANSITIONS



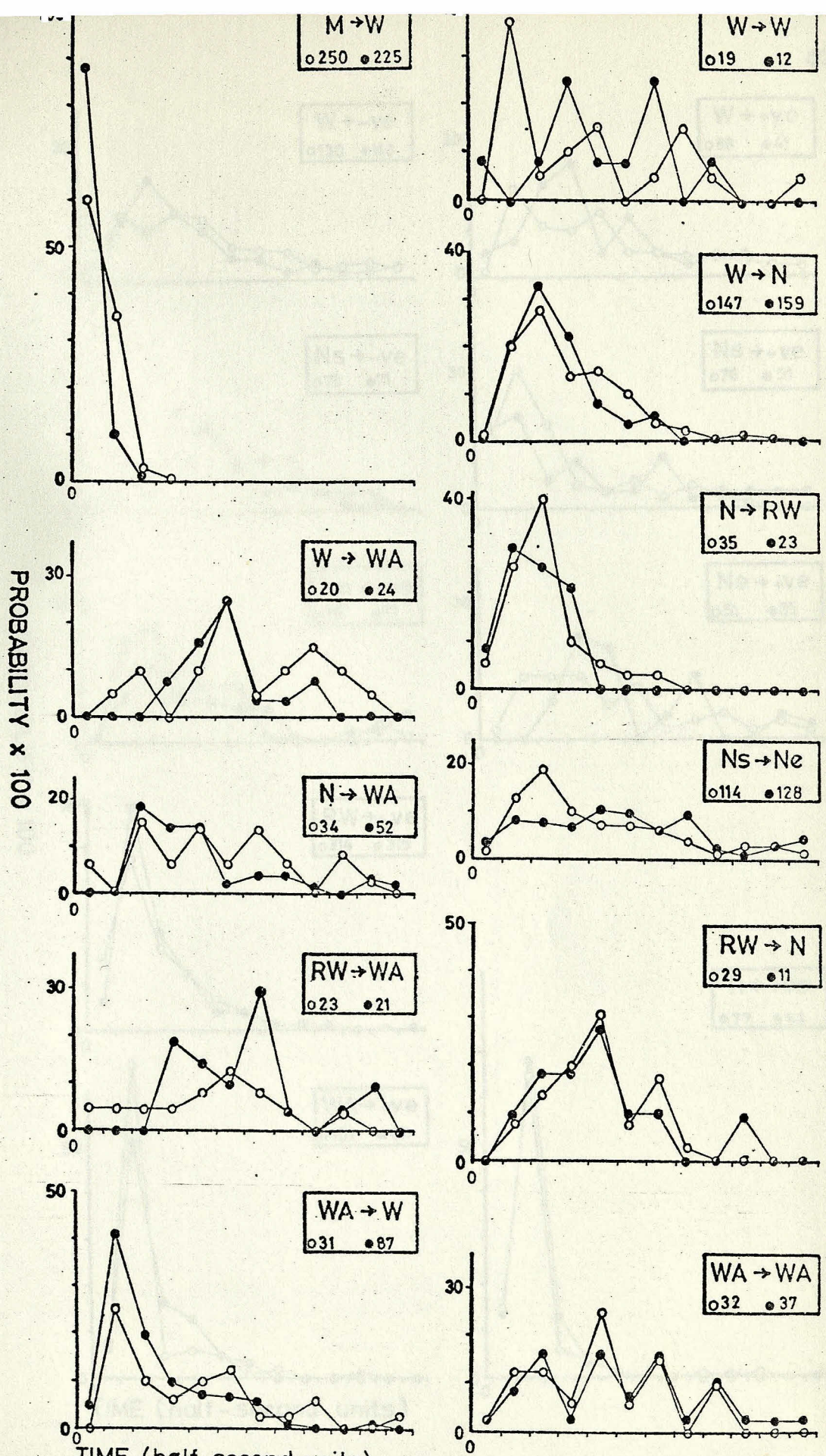
+VE INTERRUPT TRANSITIONS



TRANSITIONS OF ♂ DISPLAY ACTS

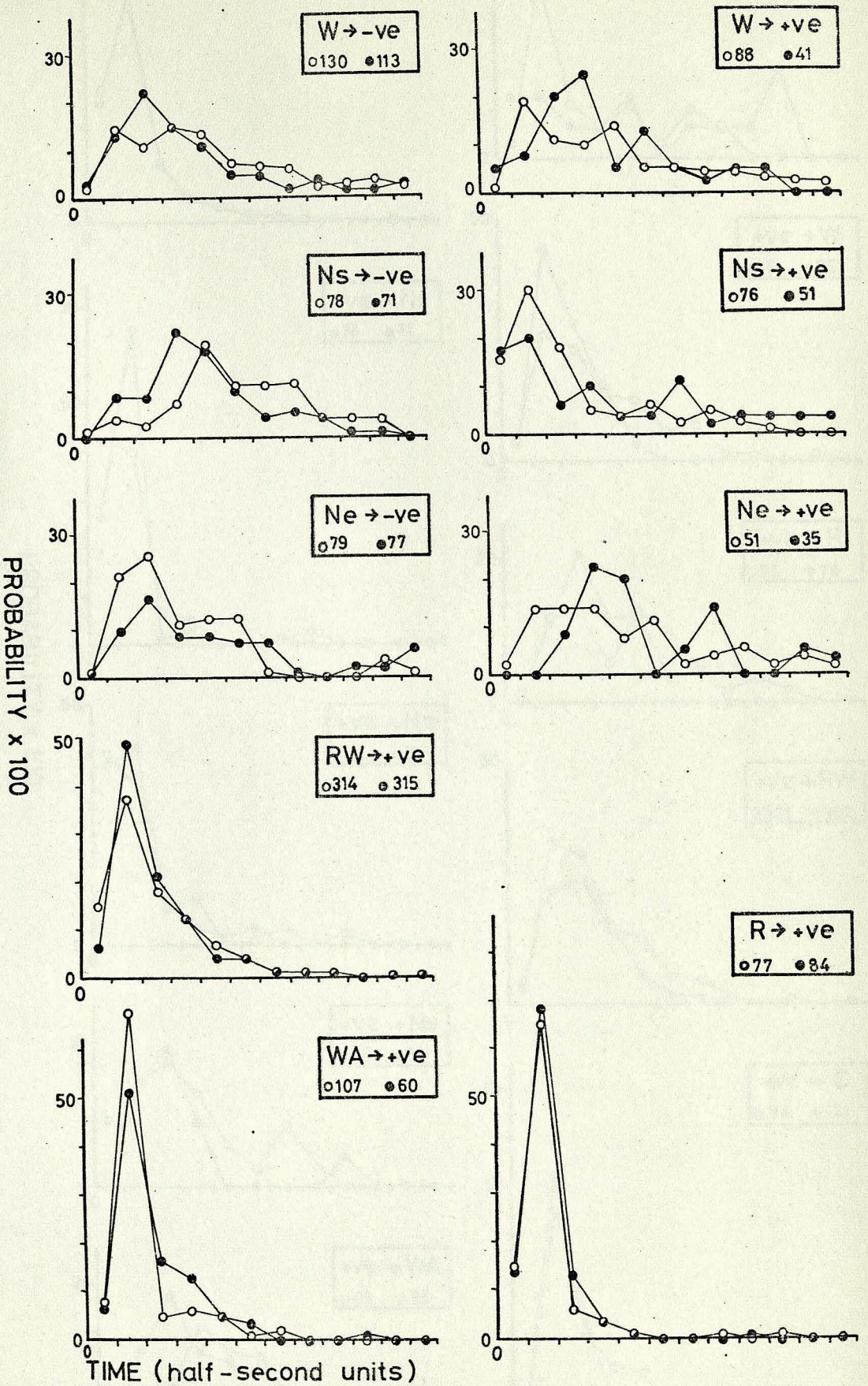
Width of lines is proportional to the frequency of transition - 1mm to 50 transitions. Lines above the horizontal read from left to right, those below read from right to left. Frequency of transition to the same act, e.g: W - W, is represented by the width of the dot on the right of each act: 1 mm to 50 transitions.
For full explanation see text.

ABBREVIATIONS: OR: Orientation; M: Move-to-the-Front; W: Whip; N: Fan; WA: Wave; R: Retreat; RW: Retreat-and-Whip; C: Creep.



PROBABILITY PLOTS:
♂ACT→♂ACT TRANSITIONS

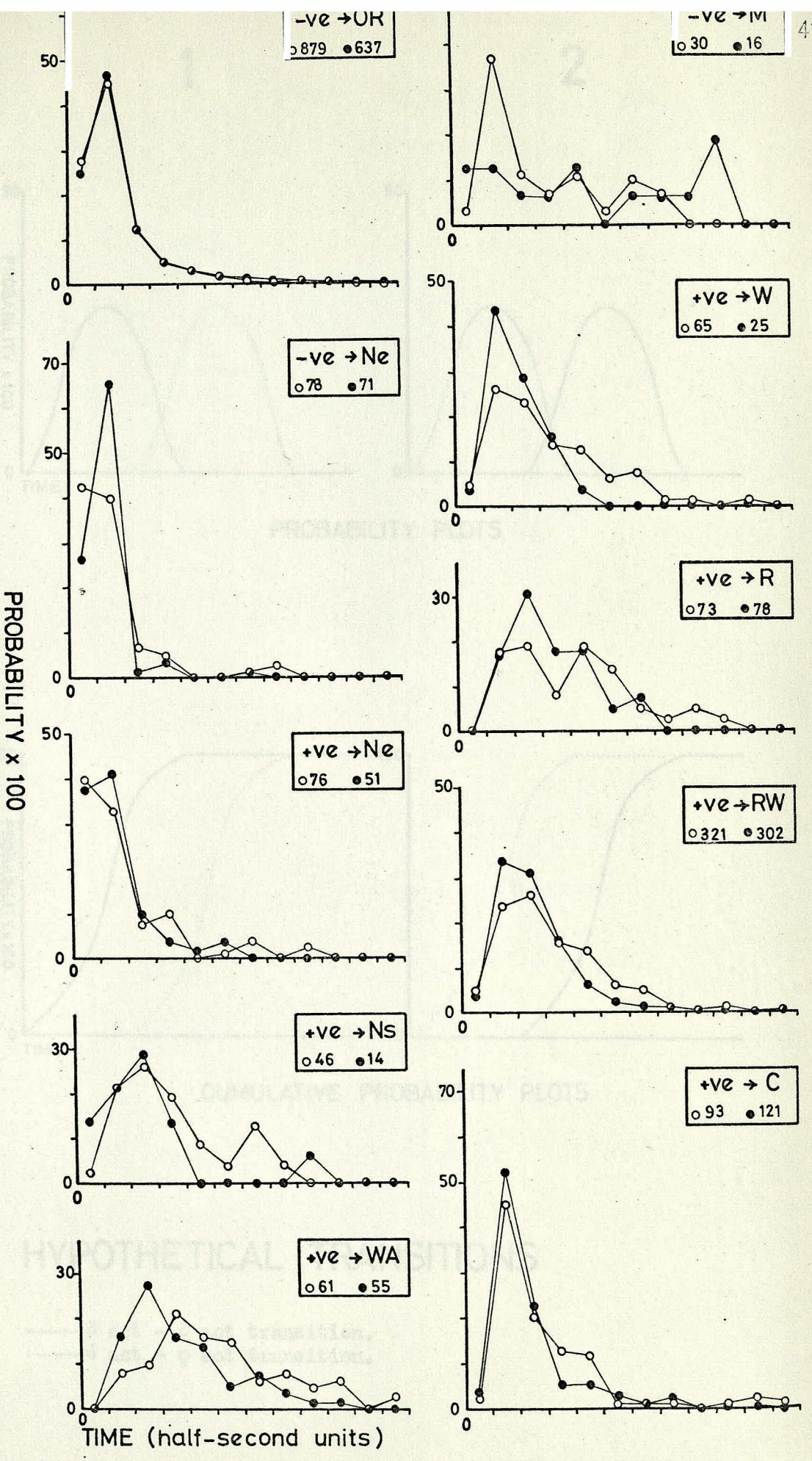
Small figures show total frequency - o1971 data, •1972 data
For raw data see Appendix 3 d.



PROBABILITY PLOTS:

♂ ACT → ♀ ACT TRANSITIONS

Small figures show total frequency - o 1971 data, • 1972 data
For raw data see Appendix 3 d.

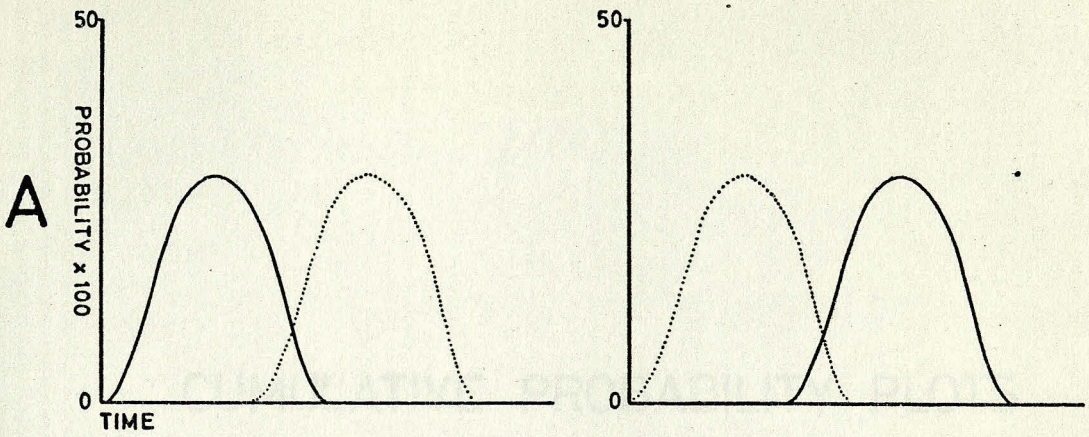


PROBABILITY PLOTS:

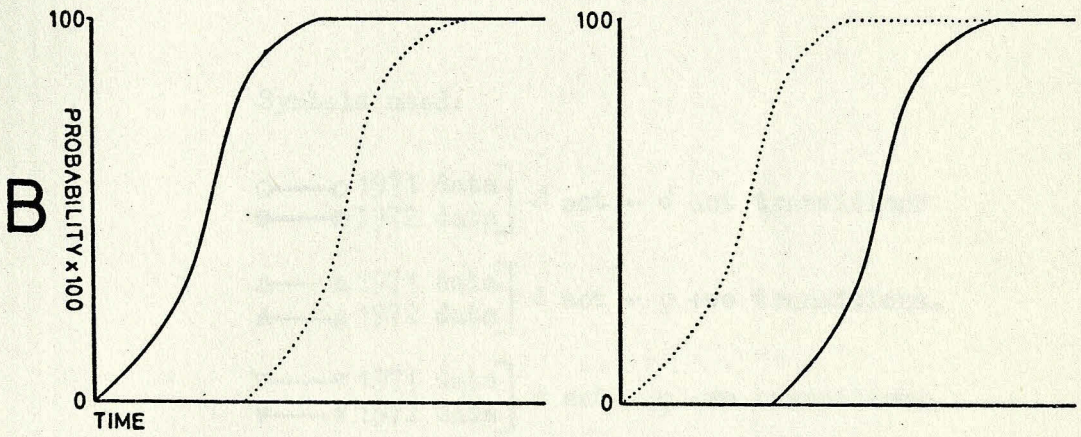
♀ ACT → ♂ ACT TRANSITIONS

Small figures show total frequency - 1971 data, 1972 data
For raw data see Appendix 3 d.

1 2



PROBABILITY PLOTS



CUMULATIVE PROBABILITY PLOTS

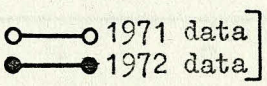
HYPOTHETICAL TRANSITIONS

——♂ act - ♂ act transition.
.....♂ act - ♀ act transition.

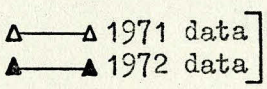
CUMULATIVE PROBABILITY PLOTS

SINGLE ORDER TRANSITIONS FROM ♂ DISPLAY ACTS

Symbols used:



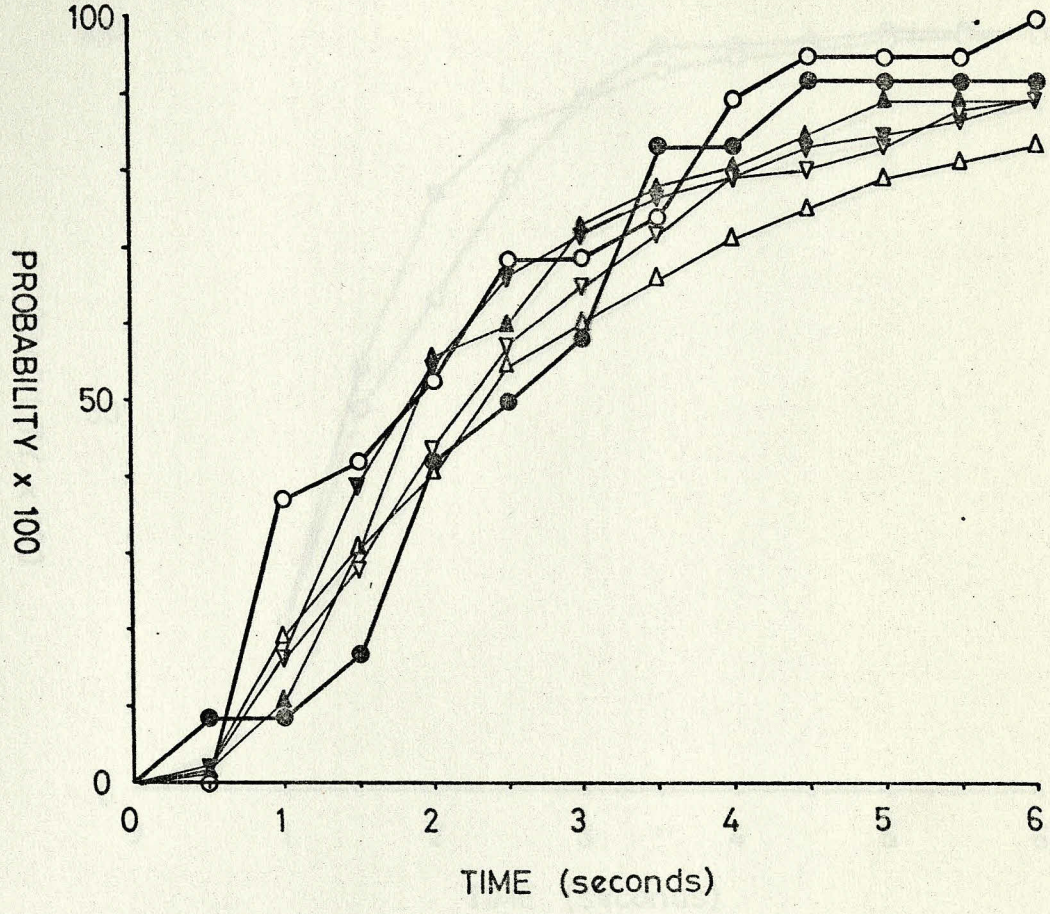
♂ act - ♂ act transitions



♂ act - ♀ +ve transitions.

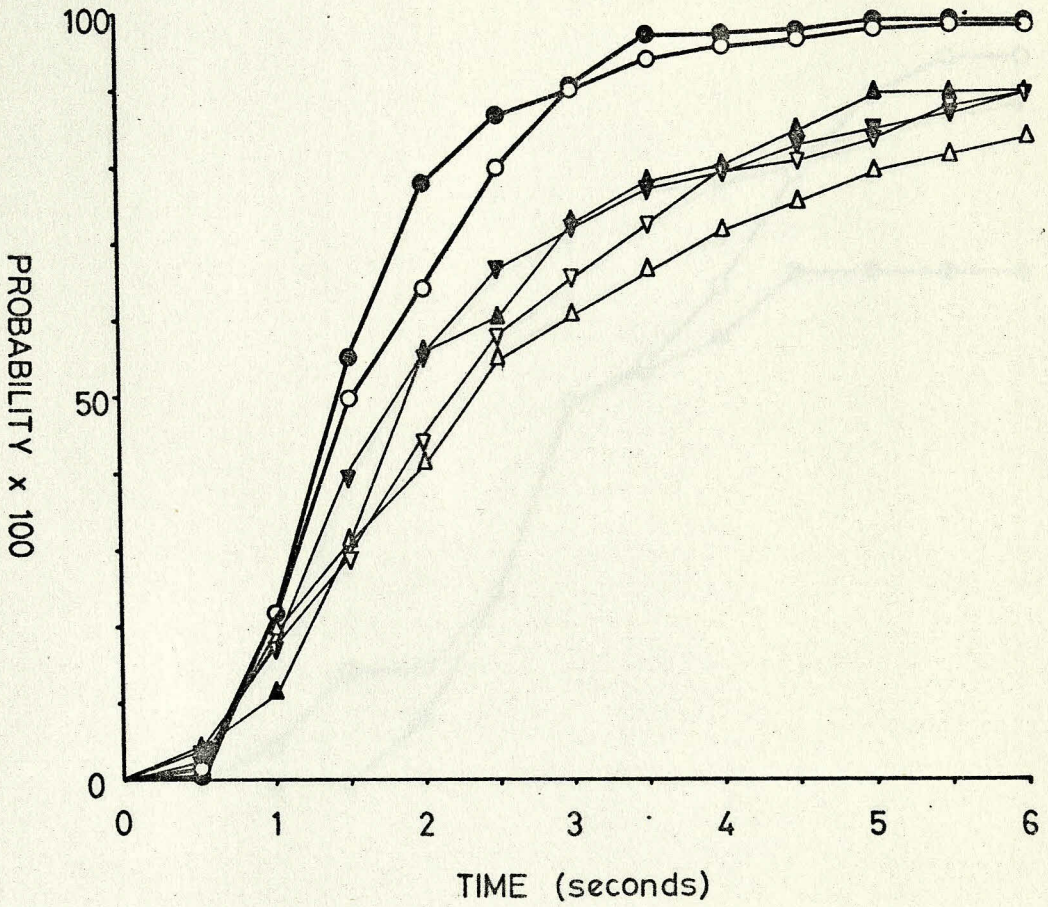


♂ act - ♀ -ve transitions.



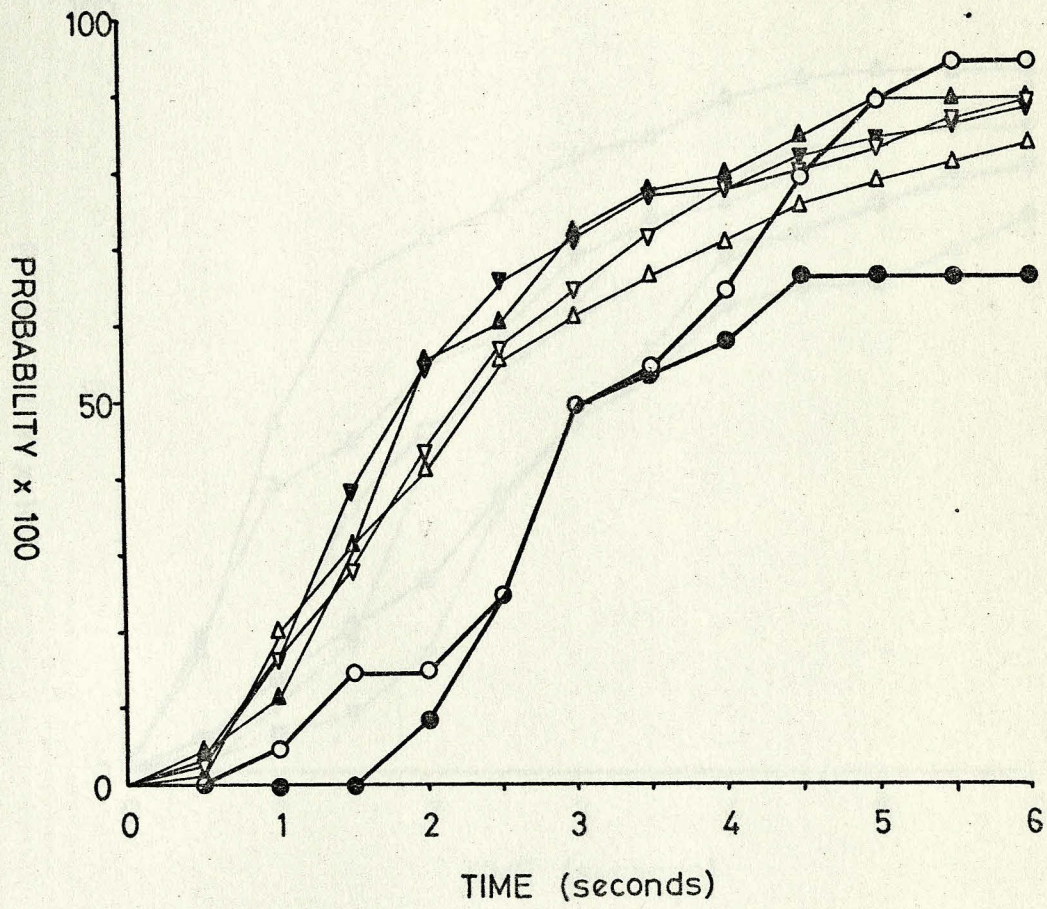
CUMULATIVE PROBABILITY PLOT:
W→W

For explanation of symbols see page 2/43.



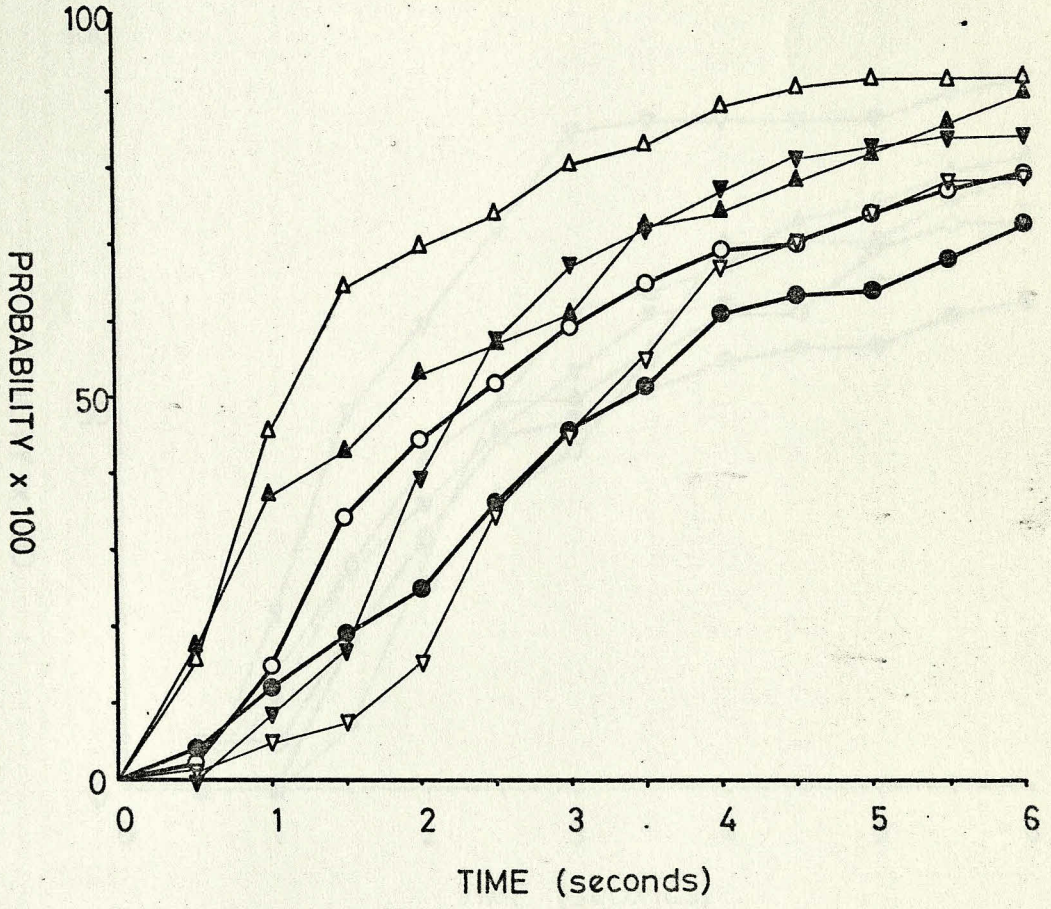
CUMULATIVE PROBABILITY PLOT: W→N

For explanation of symbols see page 2/43.



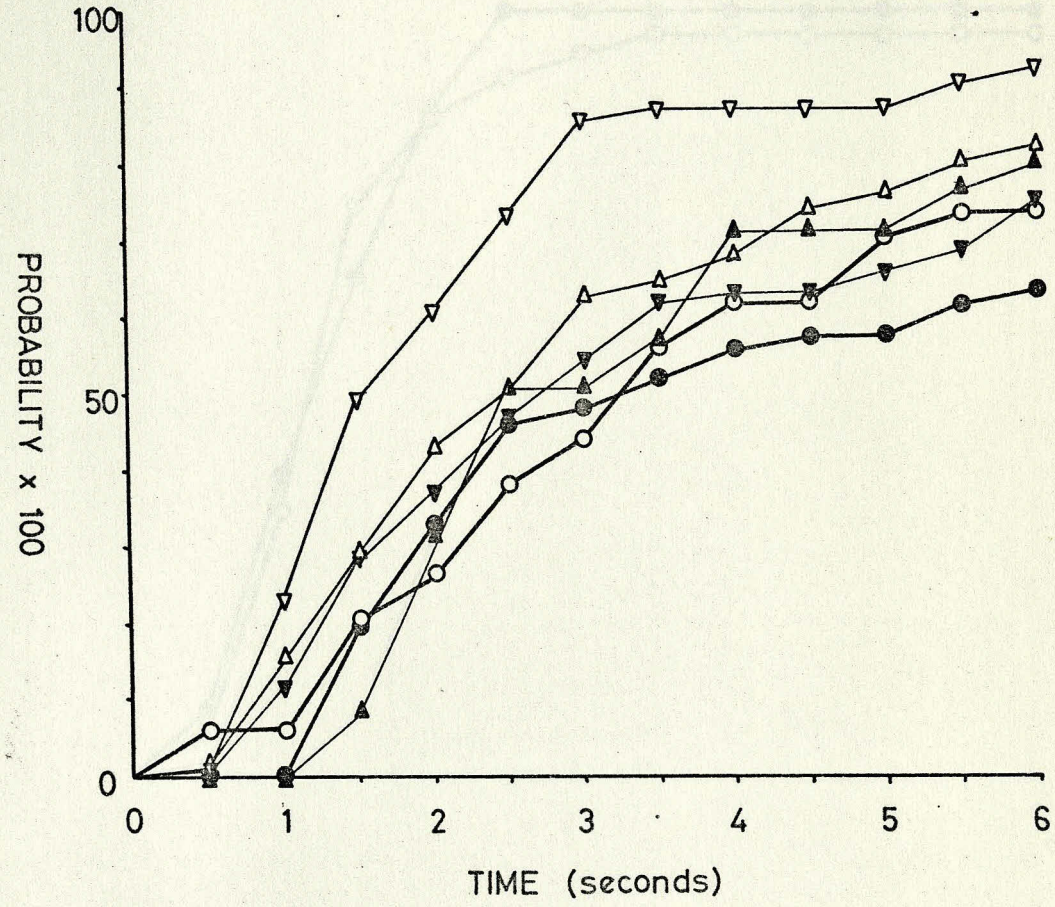
CUMULATIVE PROBABILITY PLOT:
W → WA

For explanation of symbols see page 2/43.



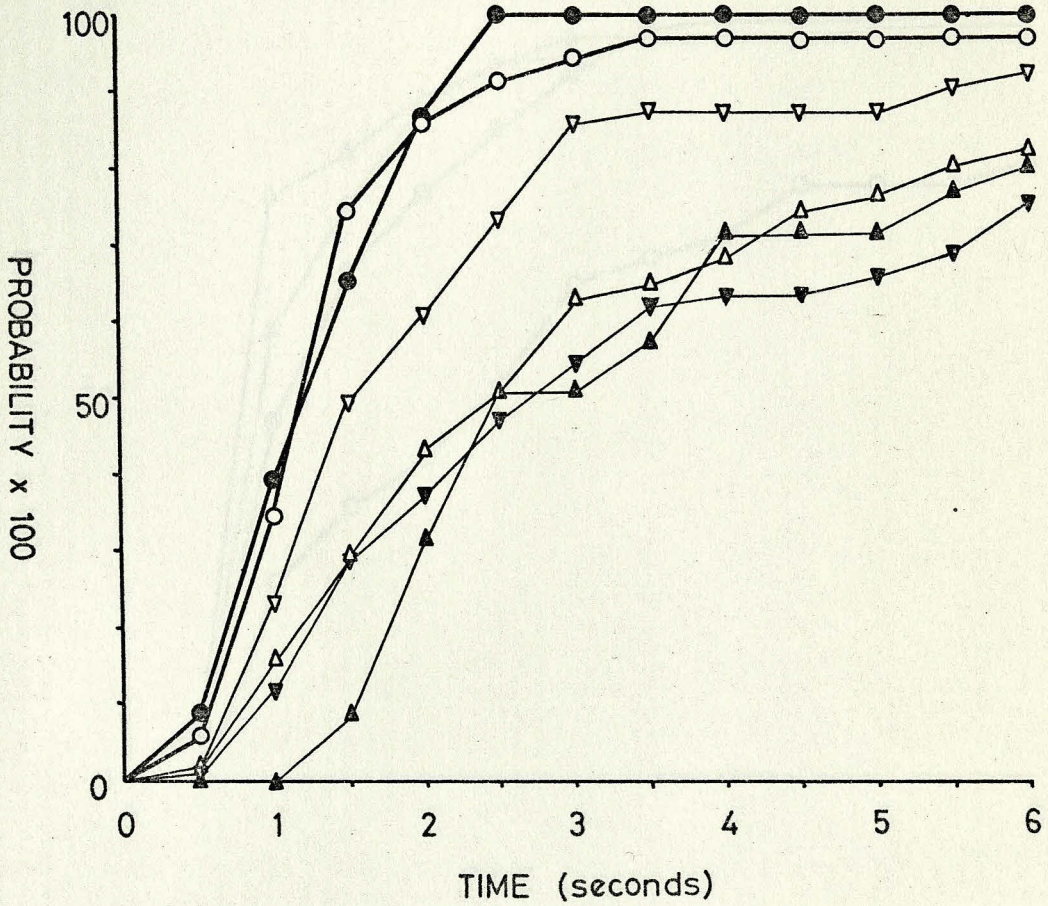
CUMULATIVE PROBABILITY PLOT: Ns → Ne

For explanation of symbols see page 2/43.



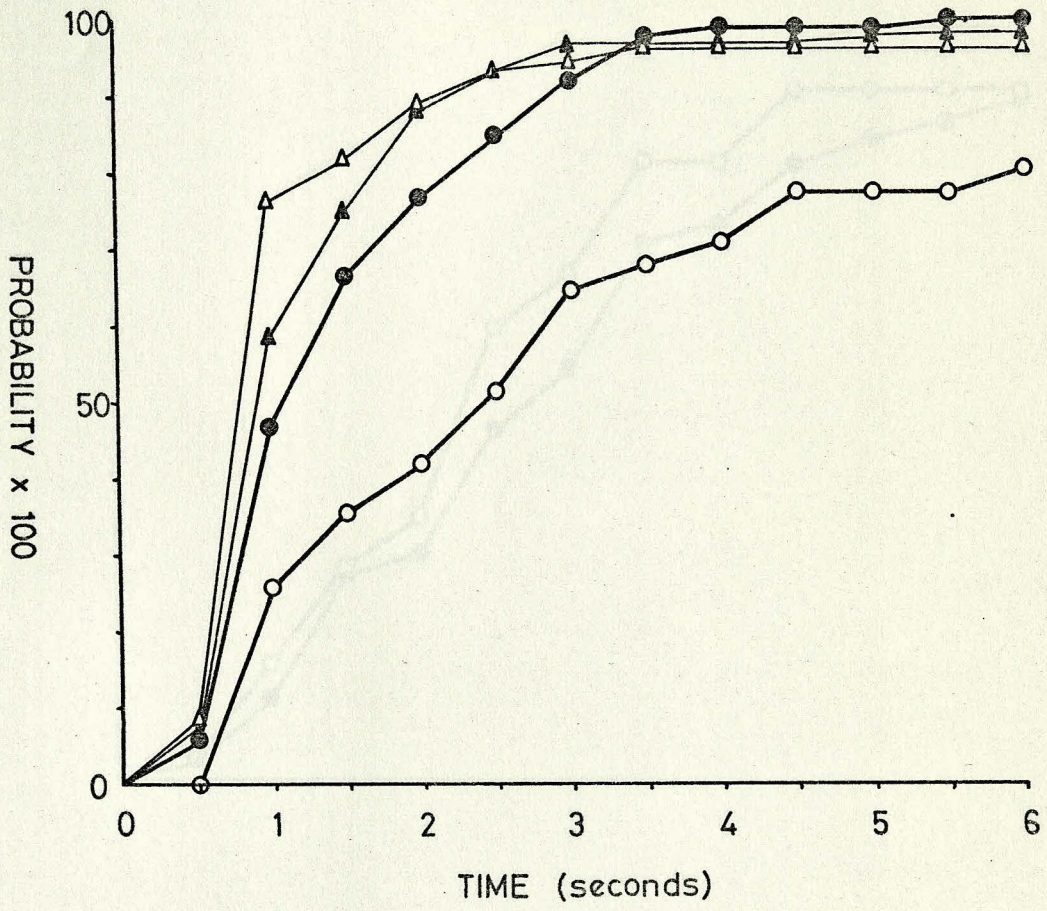
CUMULATIVE PROBABILITY PLOT: Ne → WA

For explanation of symbols see page 2/43.



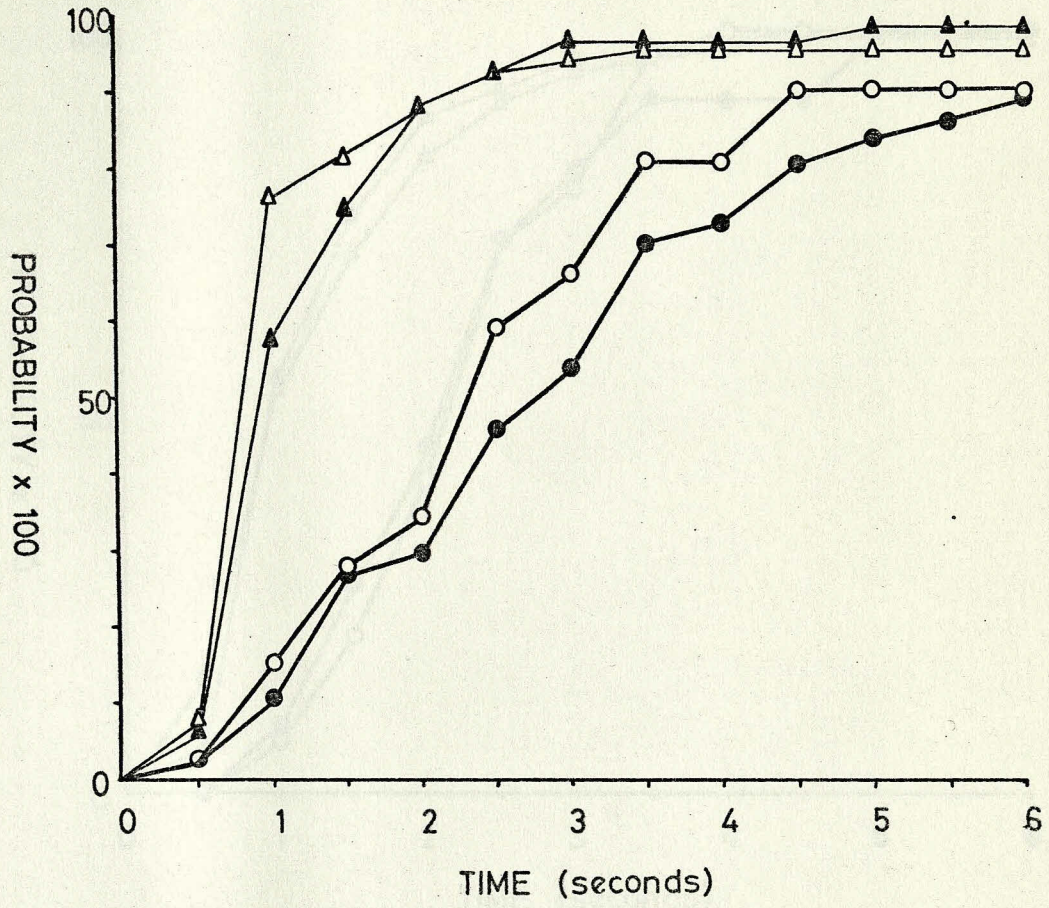
CUMULATIVE PROBABILITY PLOT: Ne → RW

For explanation of symbols see page 2/43.



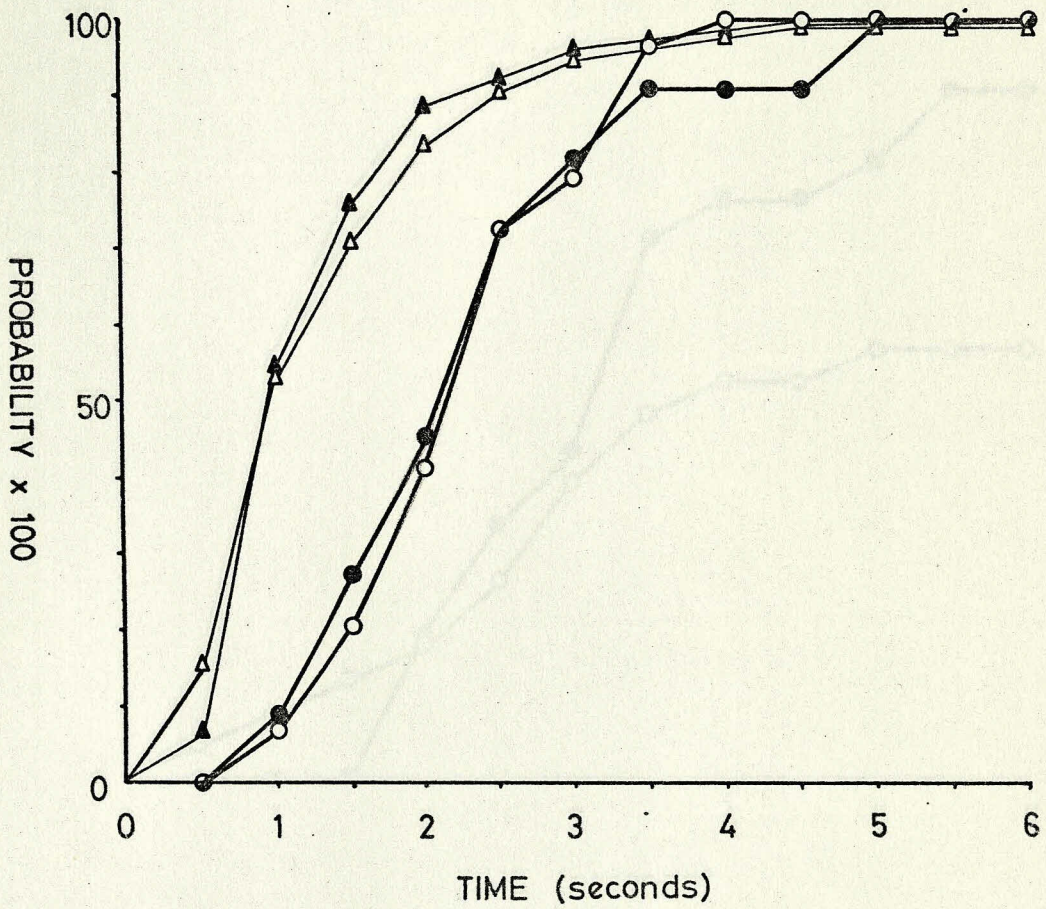
CUMULATIVE PROBABILITY PLOT:
WA →W

For explanation of symbols see page 2/43.



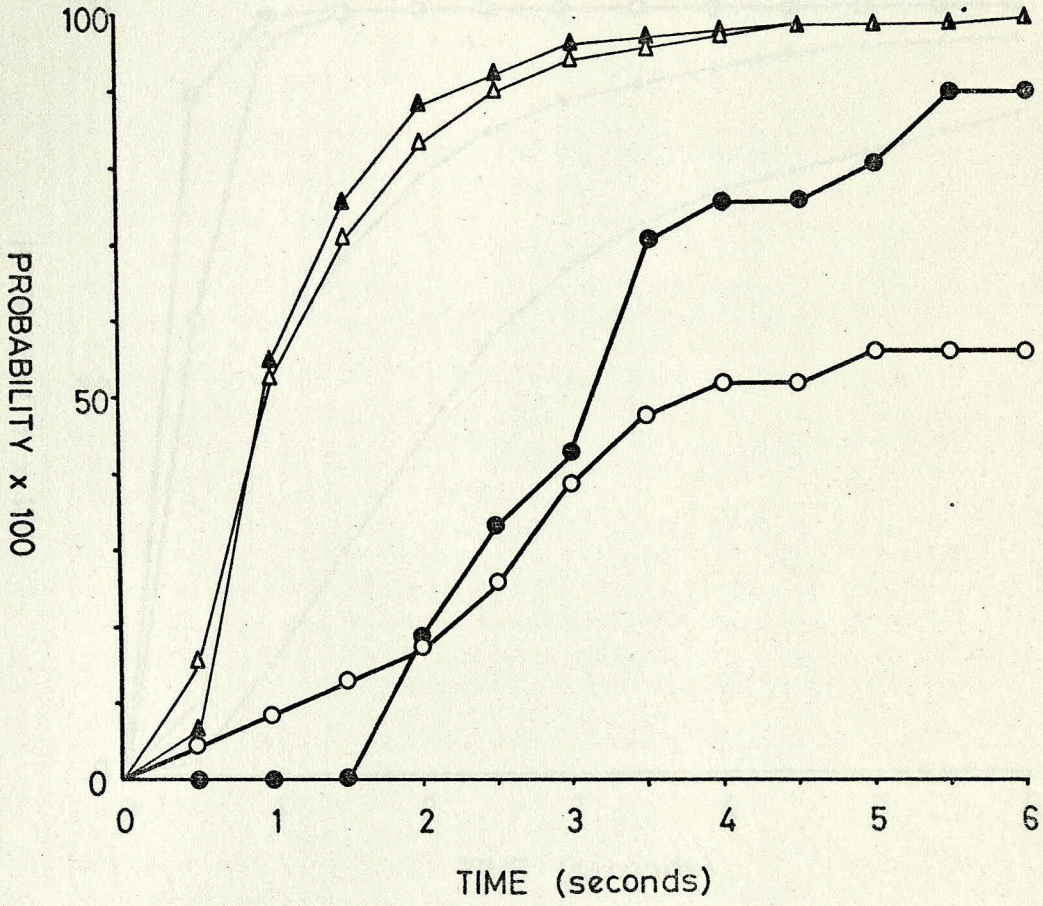
CUMULATIVE PROBABILITY PLOT: WA → WA

For explanation of symbols see page 2/43.



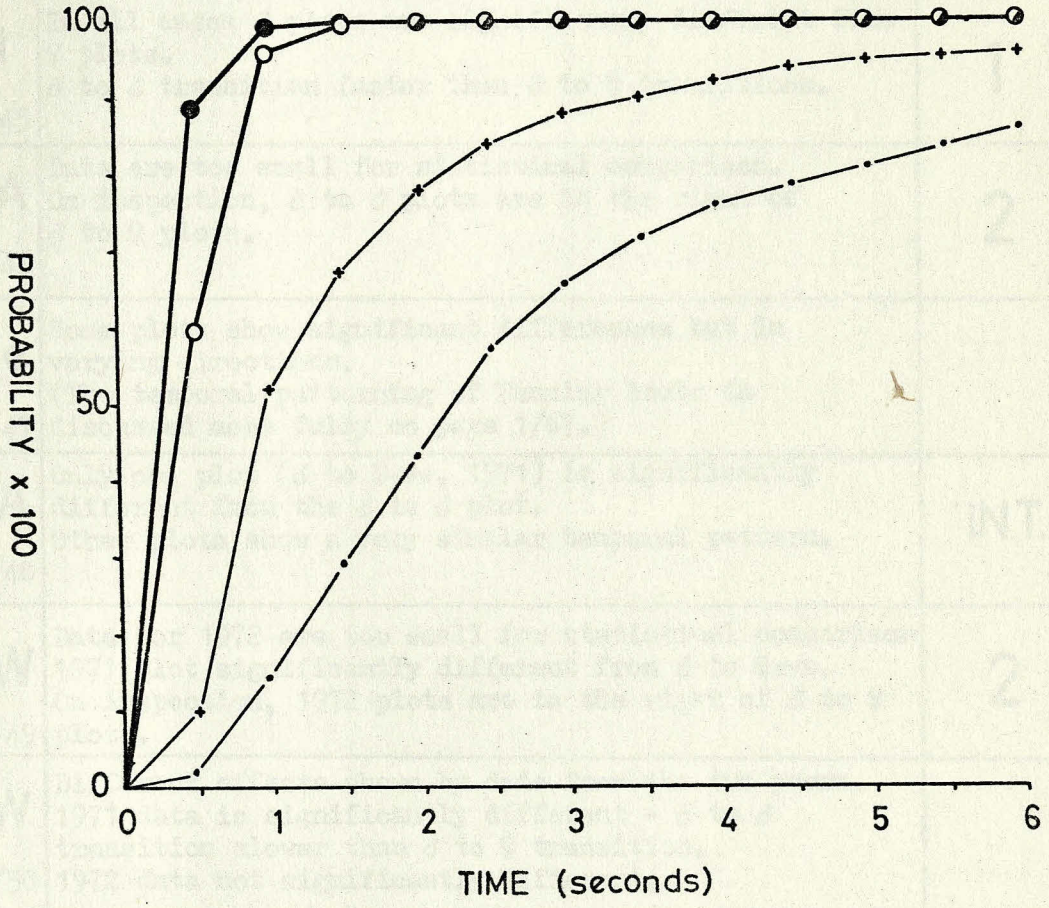
CUMULATIVE PROBABILITY PLOT: RW→N

For explanation of symbols see page 2/43.



CUMULATIVE PROBABILITY PLOT: RW→WA

For explanation of symbols see page 2/43.



CUMULATIVE PROBABILITY PLOT:

M→W

+——+ Plot derived from all ♂ act - ♀ +ve transitions.

•——• Plot derived from all ♂ act - ♀ -ve transitions.

♂ to ♂ TRANSITION	RESULTS OF COMPARISON OF ♂ to ♂ TRANSITION WITH APPROPRIATE ♂ to ♀ TRANSITIONS	CONDITION
W→W page 2/44	Data are too small for statistical comparison. On inspection, ♂ and ♀ plots show a very similar temporal pattern.	INT.
W→N page 2/45	In all cases ♂ plots are significantly different from ♀ plots. ♂ to ♂ transition faster than ♂ to ♀ transitions.	1
W→WA page 2/46	Data are too small for statistical comparison. On inspection, ♂ to ♂ plots are to the right of ♂ to ♀ plots.	2
Ns→Ne page 2/47	Some plots show significant differences but in varying directions. (The temporal patterning of Fanning bouts is discussed more fully on page 1/67.)	
N→WA page 2/48	Only one plot (♂ to ♀-ve, 1971) is significantly different from the ♂ to ♂ plot. Other plots show a very similar temporal pattern.	INT.
N→RW page 2/49	Data for 1972 are too small for statistical comparison 1971 plot significantly different from ♂ to ♀+ve. On inspection, 1972 plots are to the right of ♂ to ♀ plots.	2
WA→W page 2/50	Different effects shown by data from the two years. 1971 data is significantly different - ♂ to ♂ transition slower than ♂ to ♀ transition. 1972 data not significantly different.	
WA→WA page 2/51	Both years show a significant difference. ♂ to ♂ transition is slower than ♂ to ♀ transition.	2
RW→N page 2/52	Data are too small for statistical comparison. On inspection, ♂ to ♂ plots are to the right of ♂ to ♀ plots.	2
RW→WA page 2/53	Data are too small for statistical comparison. On inspection, ♂ to ♀ plots are to the right of ♂ to ♀ plots.	2
M→W page 2/54	Data for M to ♀ acts are virtually non-existent. In the figure the ♂ transition is compared with plots derived from ALL ♂ to ♀ transitions. Note that this transition is faster than any other ♂ to ♂ or ♂ to ♀ transition.	1

RESULTS OF COMPARISONS OF CUMULATIVE PROBABILITY PLOTS (For Statistical details see Appendix 3 f.)

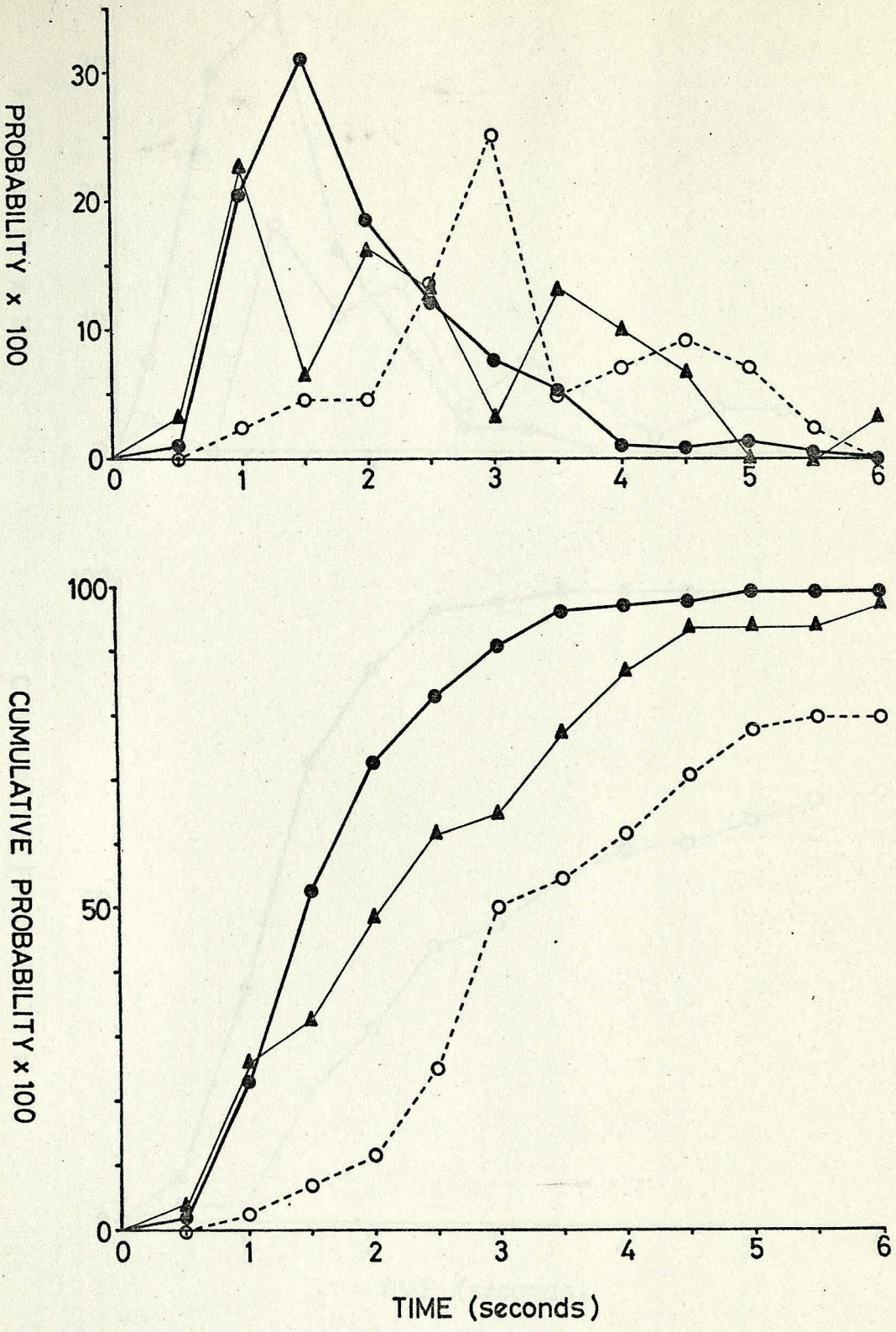
CONDITION 1: ♂ to ♂ transition has earlier peak than ♂ to ♀ transition.
CONDITION 2: ♂ to ♂ transition has later peak than ♂ to ♀ transition.
INT: Intermediate situation in which ♂ to ♂ and ♂ to ♀ transitions have similar temporal distributions.

♂ ACT	MOST COMMON TRANSITION	H (bits)
M	→W 95%	0·335
W	→N 71%	1·477
WA	→W 49%	1·937
R	→N 48%	2·398
RW	→WA 38%	2·213
N	→WA 33%	2·688

PREDICTABILITY OF UNINTERRUPTED TRANSITIONS FROM ♂ DISPLAY ACTS

The middle column shows the most frequently occurring uninterrupted transition from each male act, and the percentage of all observed uninterrupted transitions from that act accounted for by that transition.

The right-hand column shows a measure H (measured in bits) which is a measure of the uncertainty with which uninterrupted transitions from each act can be predicted. If a transition is 100% predictable, H = 0. (For derivation of H see Appendix 3g.)

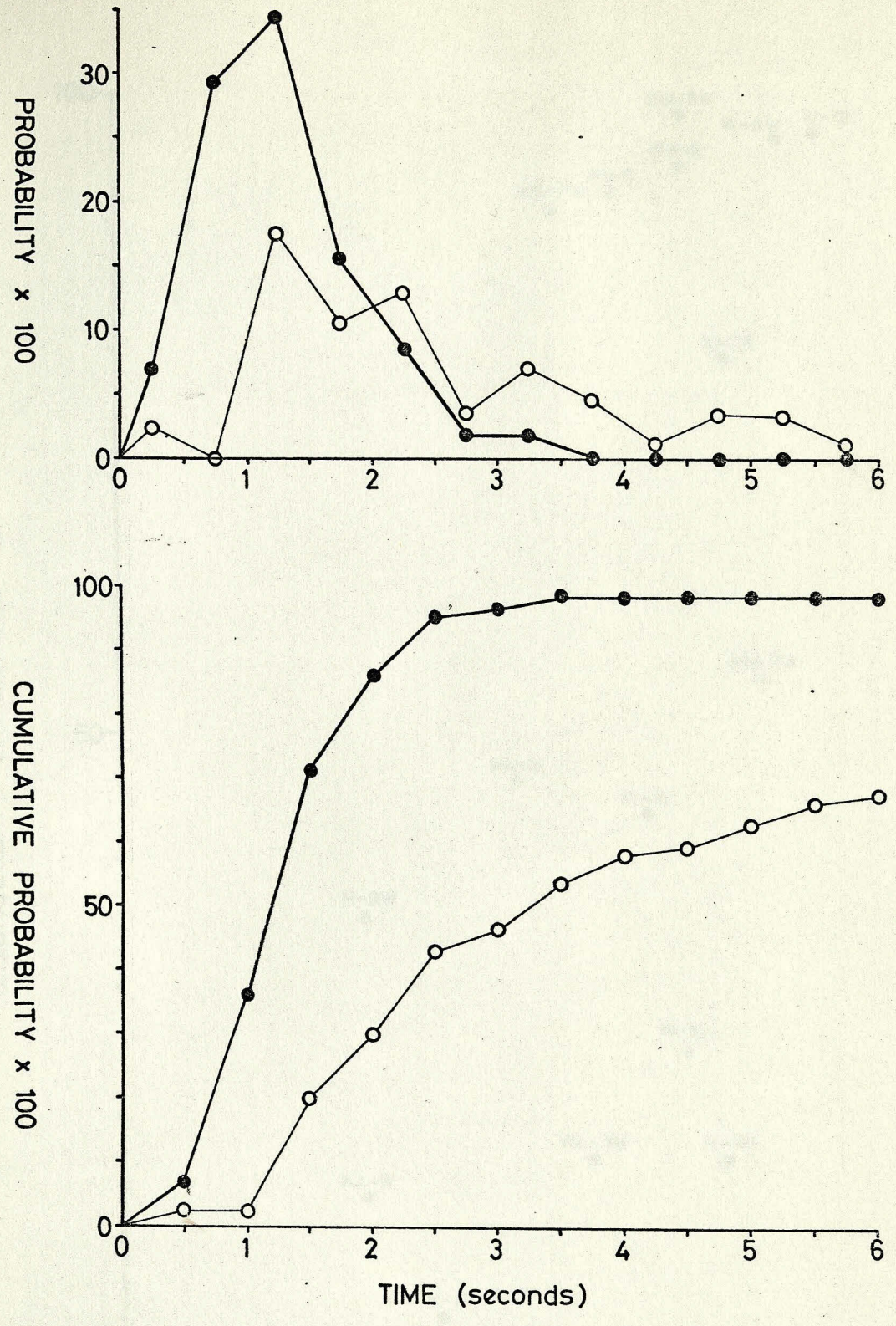


UNINTERRUPTED ♂ TRANSITIONS FROM WHIP

W to N
W to W
W to WA

1971 and 1972 data combined.

For raw data see Appendix 3 d.

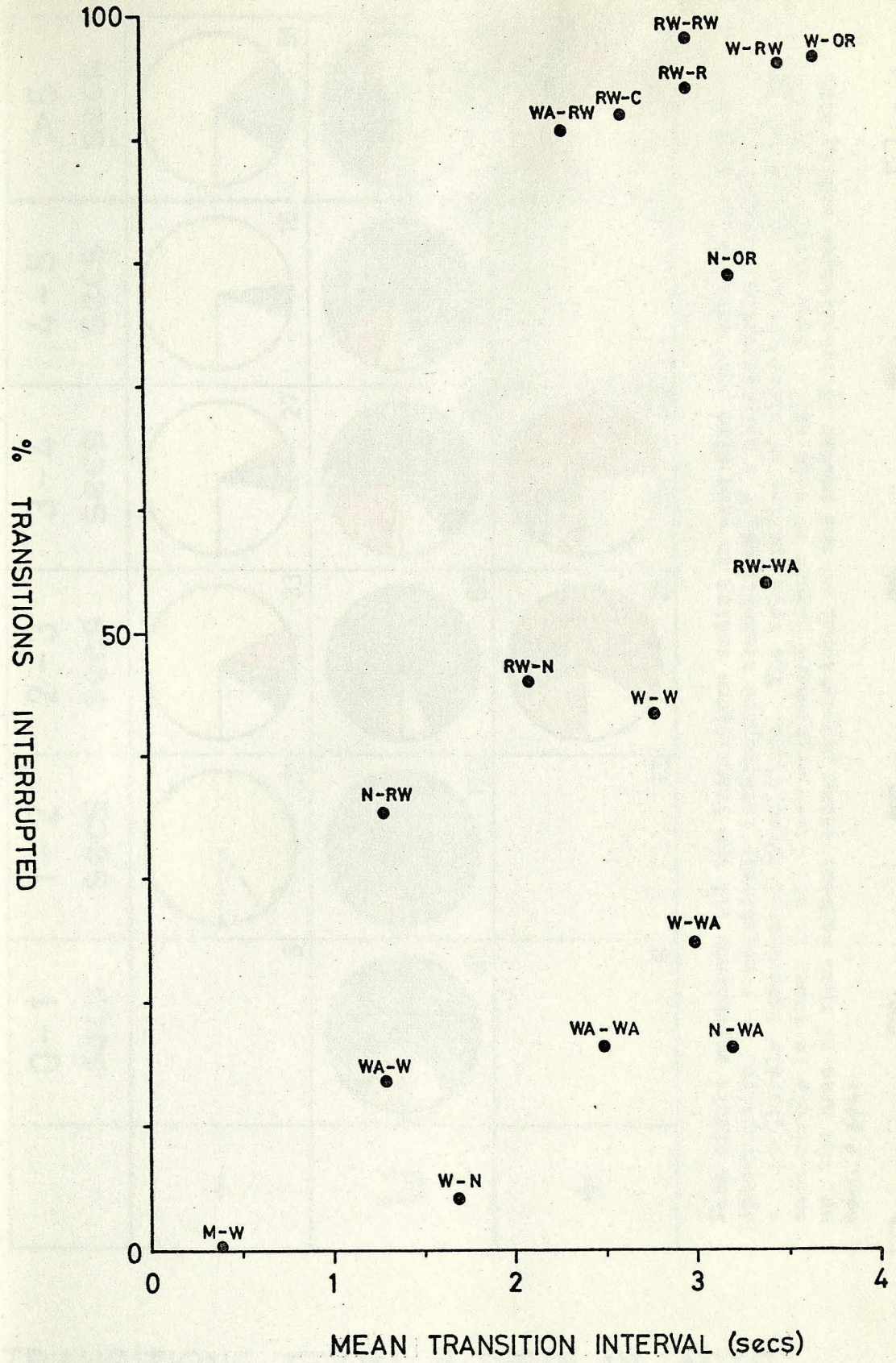


UNINTERRUPTED ♂ TRANSITIONS FROM FAN

N to RW
N to WA

1971 and 1972 data combined.

For raw data see Appendix 3 d.



TRANSITIONS BETWEEN ♂ ACTS

For raw data see Appendix 3 h.

TRANSITIONS FROM ♂ DISPLAY ACTS

1: FROM WHIP

For raw data see Appendix 3i.

TRANSITIONS FROM ♂ DISPLAY ACTS

2: FROM WAVE

For raw data see Appendix 3i.

Each circle represents all the transitions ending in each time unit after a particular ♀ interruption. - : negatively interrupted transitions, U : uninterrupted transitions, + : positively interrupted transitions. The total number of observations represented by each circle is shown in the lower right-hand corner of each cell. Each circle is divided up, the area of each segment being proportional to the number of transitions ending with each ♂ act:

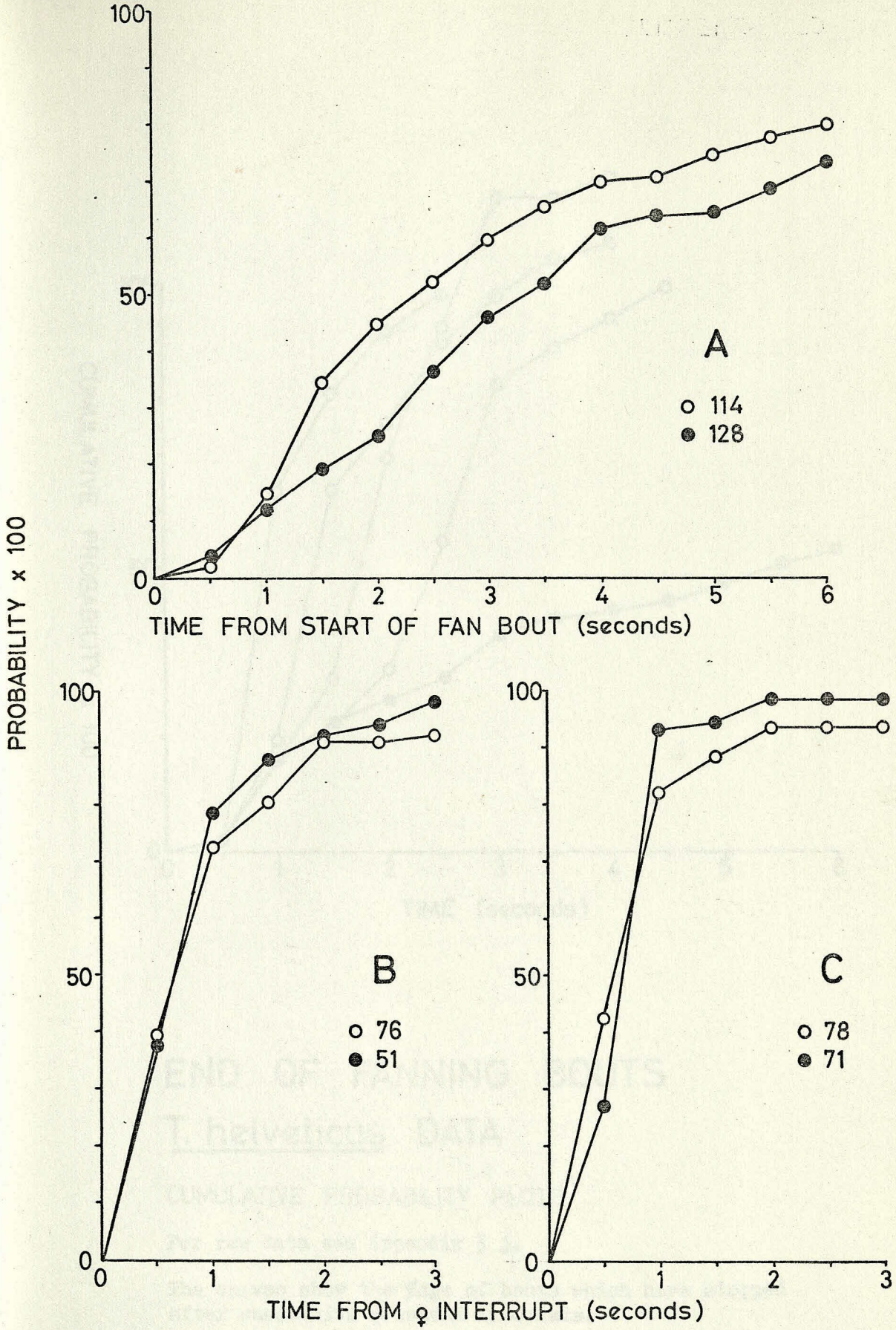
TRANSITIONS FROM ♂ DISPLAY ACTS
3: FROM RETREAT-AND-WHIP

For raw data see Appendix 3i.

TRANSITIONS FROM ♂ DISPLAY ACTS

4: FROM FAN

For raw data see Appendix 3i.

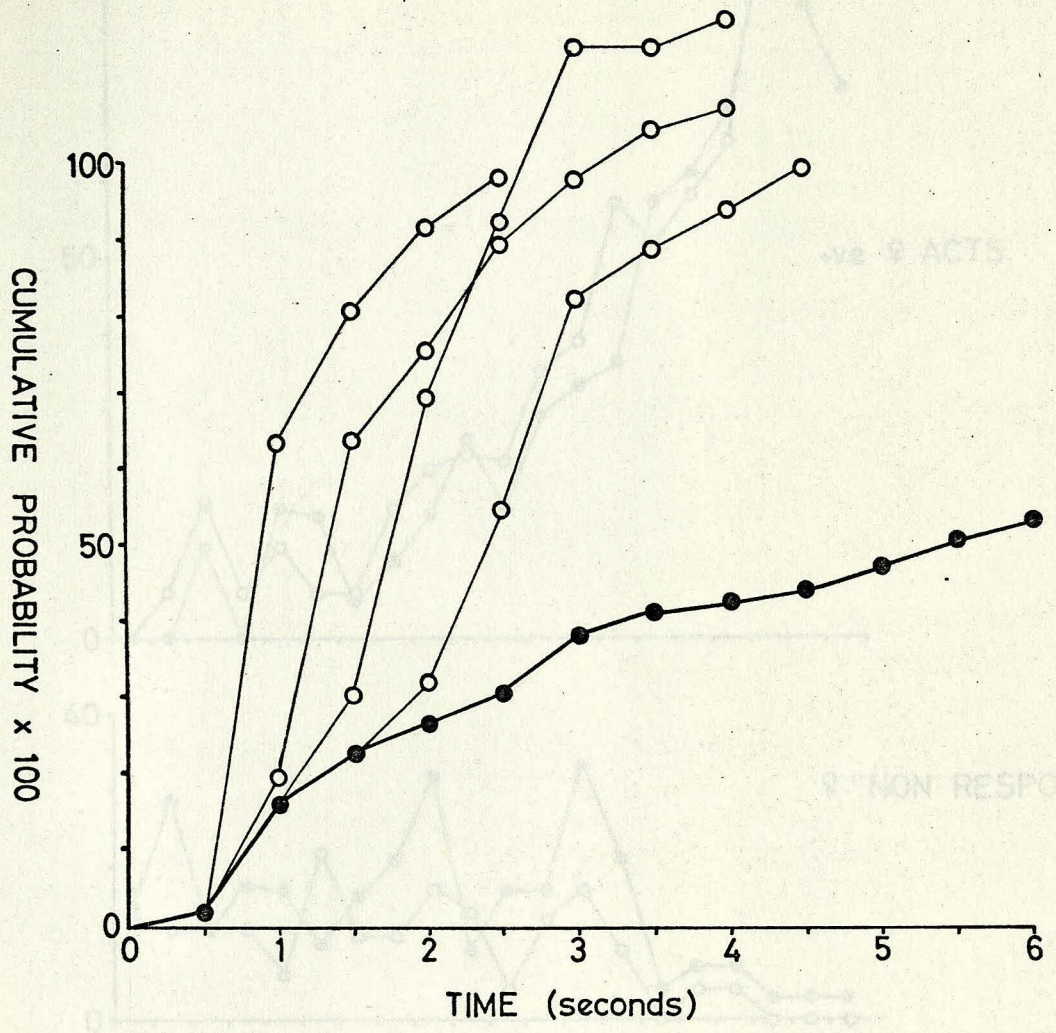


END OF FANNING BOUTS

CUMULATIVE PROBABILITY PLOTS

A: Uninterrupted bouts. B: +ve Interrupt bouts. C: -ve Interrupt bouts

o: 1971 data. ●: 1972 data. For raw data see Appendix 3 d.



END OF FANNING BOUTS

T. helveticus DATA

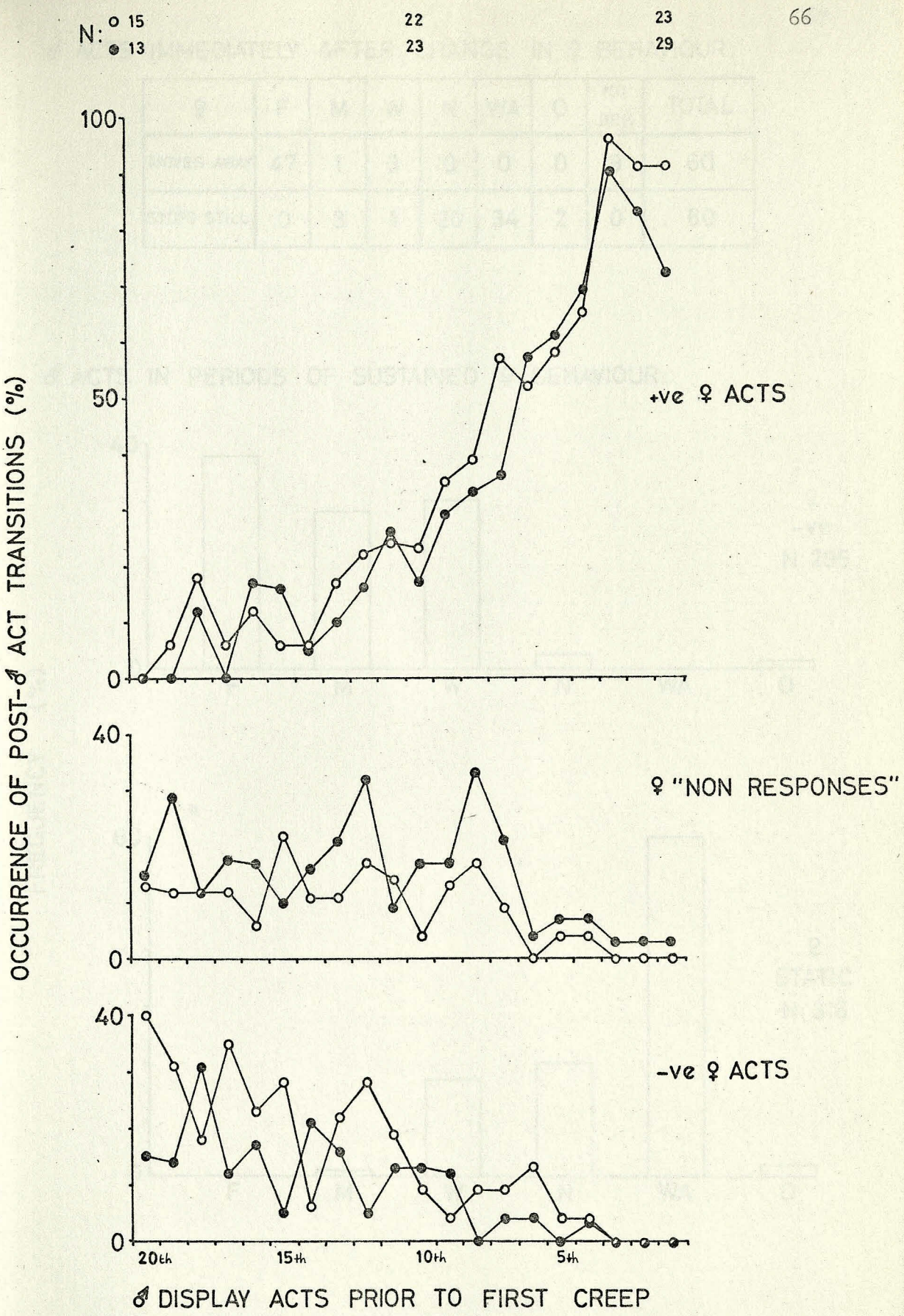
CUMULATIVE PROBABILITY PLOTS

For raw data see Appendix 3 j.

The curves show the %age of bouts which have stopped after successive $\frac{1}{2}$ second intervals.

●——● Uninterrupted bouts.
○——○ Bouts interrupted during the $\frac{1}{2}$ second interval in which the curve begins to diverge from the uninterrupted curve.

The ordinate of each Interrupted curve has its origin at the point where the Interrupted curve and the Uninterrupted curve diverge.



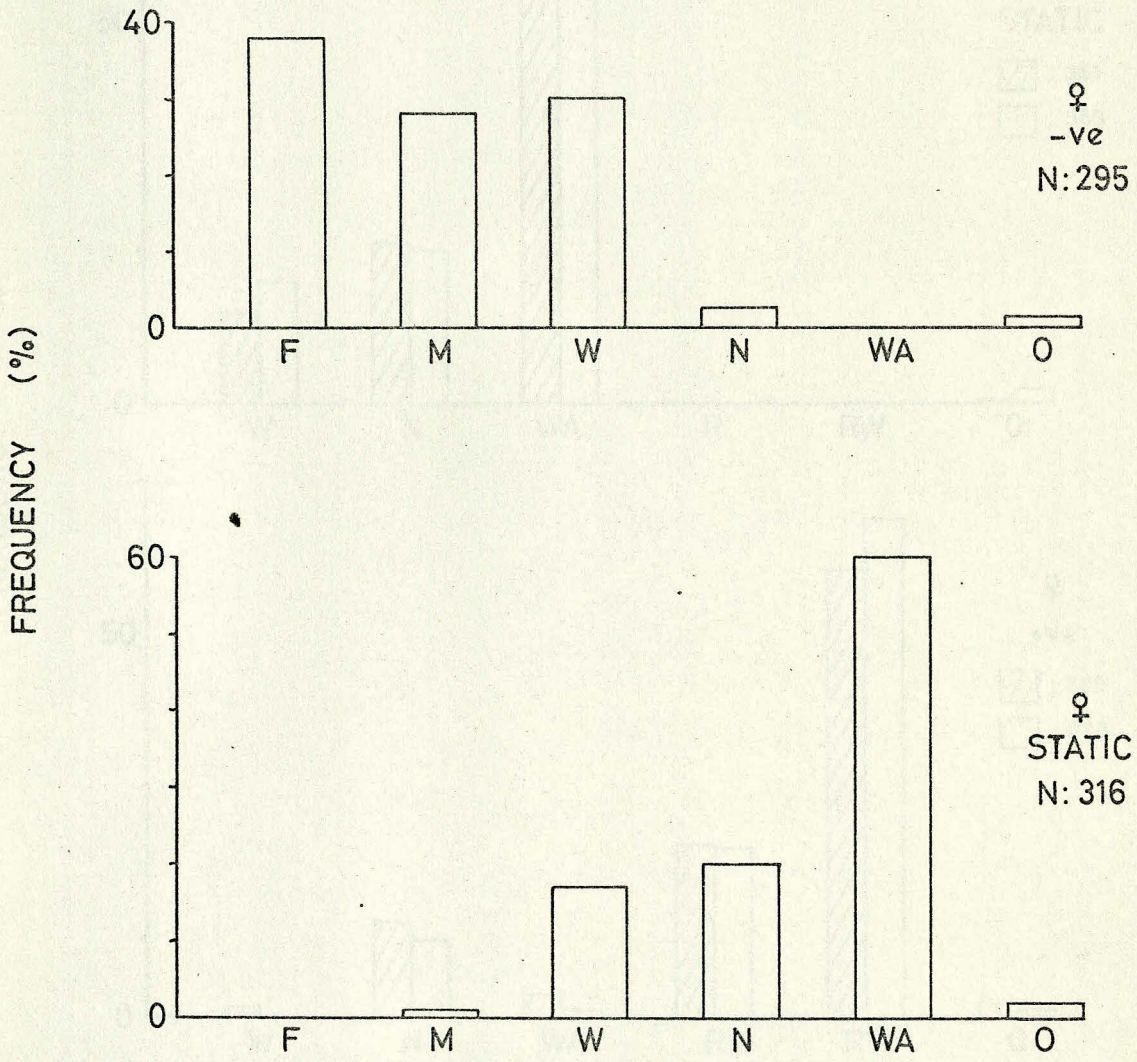
♀ ACTS IN TRANSITIONS AFTER ♂ DISPLAY ACTS

○: 1971 data. ●: 1972 data. For raw data see Appendix 3 k.

♂ ACTS IMMEDIATELY AFTER CHANGE IN ♀ BEHAVIOUR:

♀	F	M	W	N	WA	O	NO BEH.	TOTAL
MOVES AWAY	47	1	3	0	0	0	9	60
STOPS STILL	0	3	1	20	34	2	0	60

♂ ACTS IN PERIODS OF SUSTAINED ♀ BEHAVIOUR:



THE NEGATIVE/STATIC EXPERIMENT

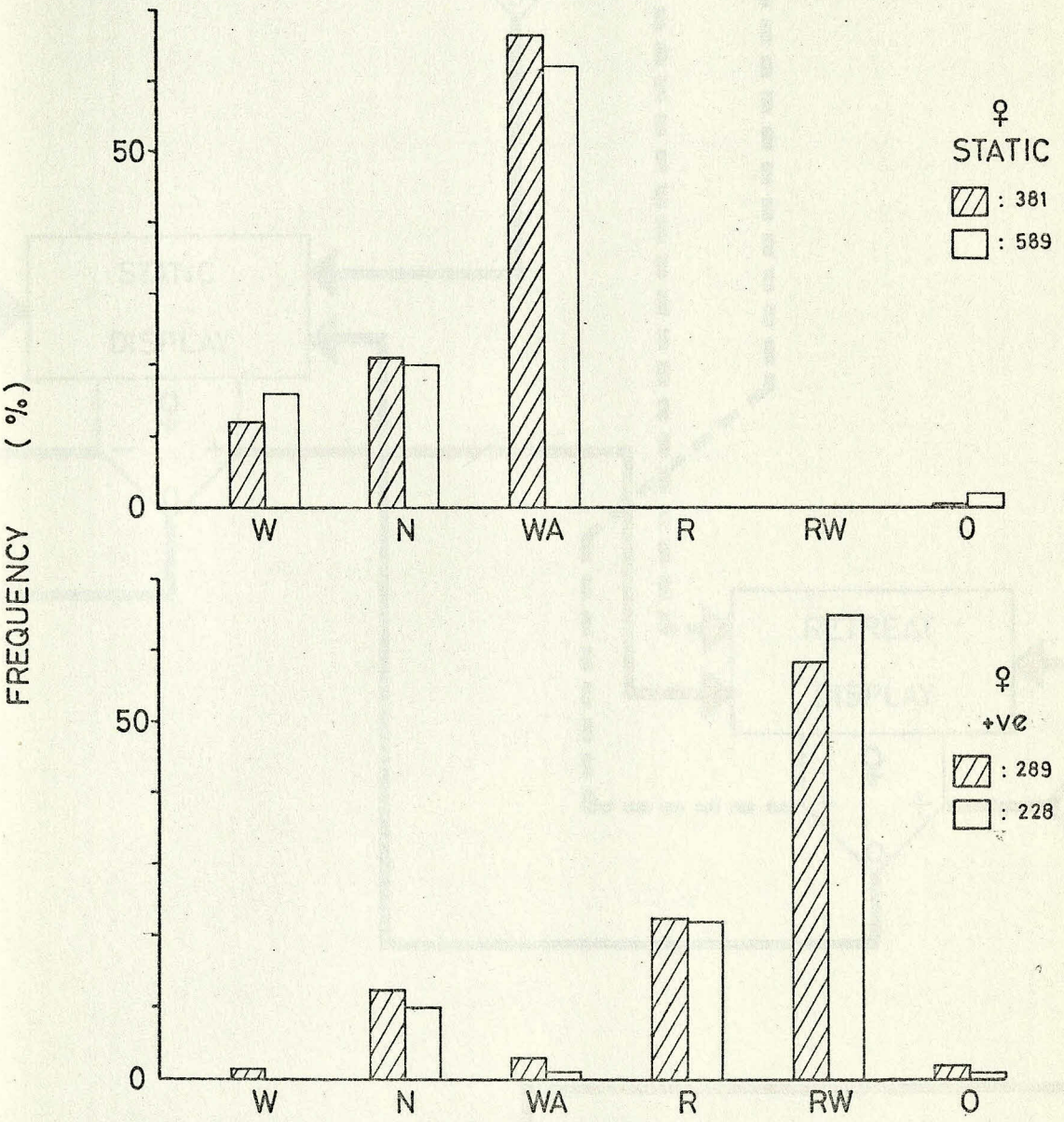
F: Follow. O: Other behaviours.

For raw data see Appendix 3 1.

♂ ACTS IMMEDIATELY AFTER CHANGE IN ♀ BEHAVIOUR:

♀	EXPT	W	N	WA	R	RW	O	TOTAL
STOPS STILL	1	4	26	28	0	0	2	60
	2	8	19	33	0	0	0	60
APPROACHES	1	2	0	2	2	53	1	60
	2	0	0	1	0	59	0	60

♂ ACTS IN PERIODS OF SUSTAINED ♀ BEHAVIOUR:

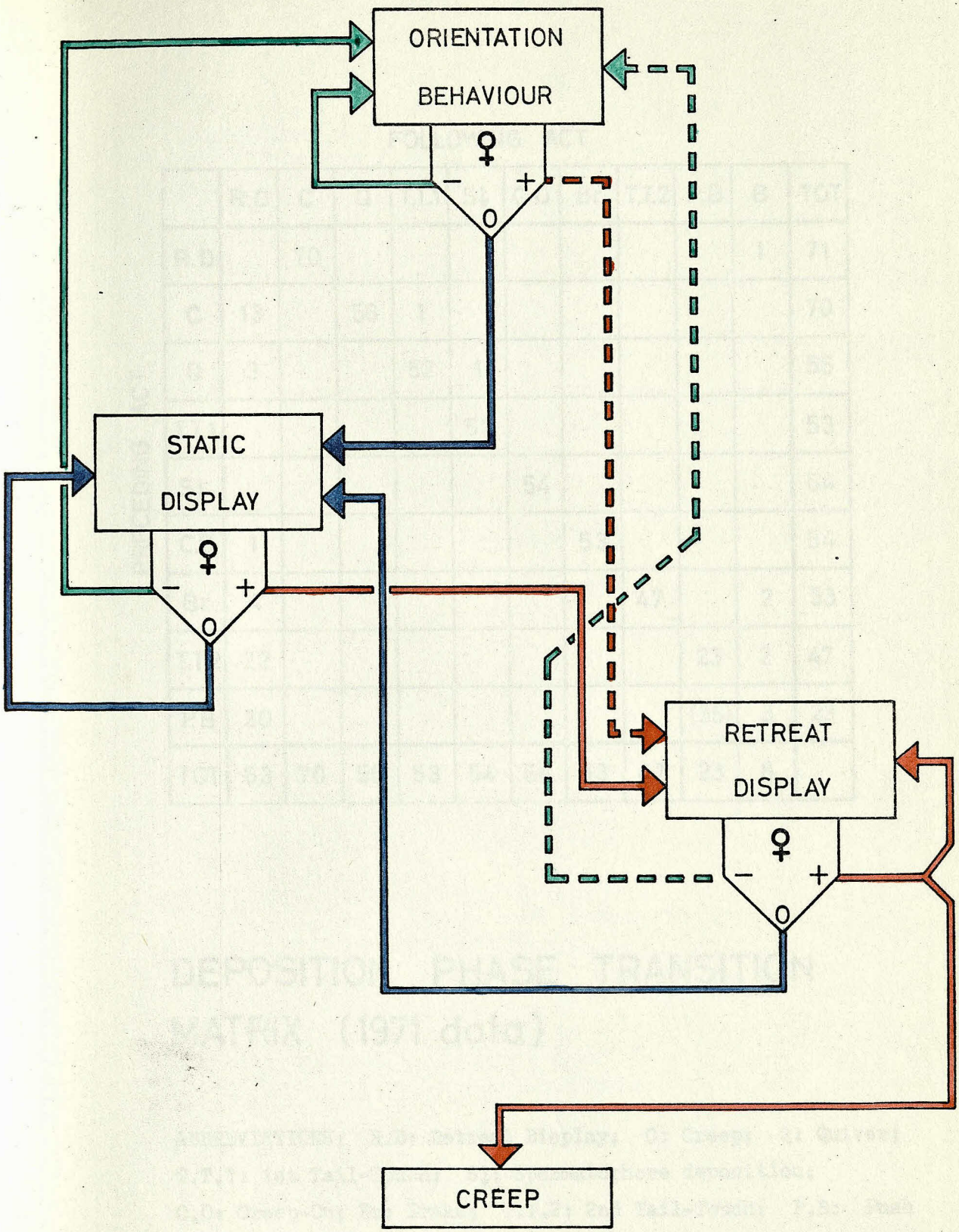


THE STATIC/POSITIVE EXPERIMENT

EXPT. 1: 20 secs / 20 secs SCHEDULE ▨

EXPT. 2: 30 secs / 10 secs SCHEDULE □

For raw data see Appendix 3 1.



SUMMARY OF THE RESULTS OF THE ORIENTATION/DISPLAY EXPERIMENTS

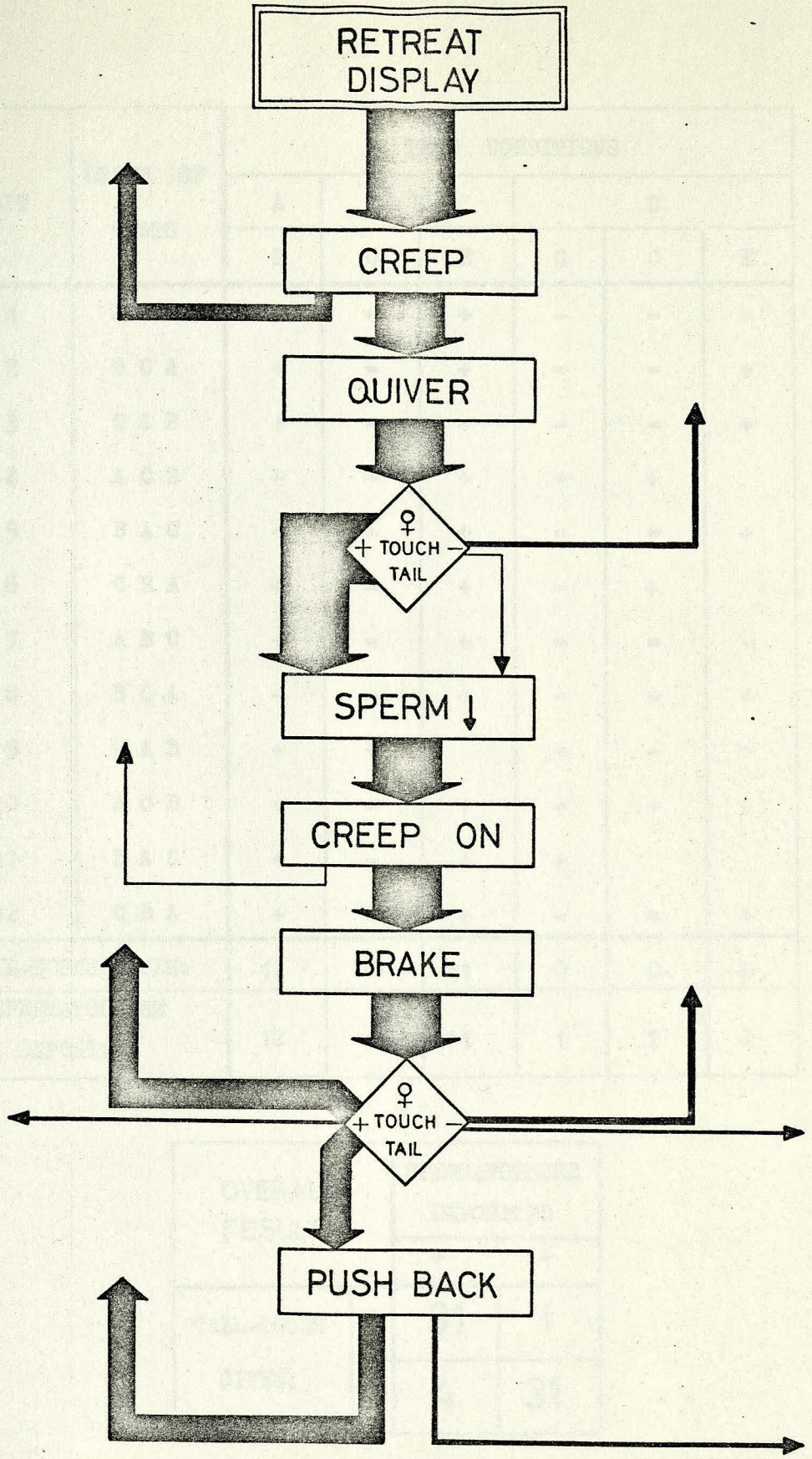
FOLLOWING ACT

PRECEDING ACT	R.D	C	Q	T.T.1	S↓	C.O	Br	T.T.2	P.B	B	TOT
R.D		70								1	71
C	13		56	1							70
Q	3			52	1						56
T.T.1					53						53
S↓						54					54
C.O	1						53				54
Br	4							47		2	53
T.T.2	22								23	2	47
P.B	20								(35)	3	23
TOT	63	70	56	53	54	54	53	47	23	8	

DEPOSITION PHASE TRANSITION MATRIX (1971 data)

ABBREVIATIONS: R.D: Retreat Display; C: Creep; Q: Quiver; T.T.1: 1st Tail-Touch; S↓: Spermatophore deposition; C.O: Creep-On; Br: Brake; T.T.2: 2nd Tail-Touch; P.B: Push Back; B: Breathe; TOT: Totals.

All acts are ♂ acts except T.T.1 and T.T.2.



TRANSITIONS OF DEPOSITION PHASE ACTIONS

T. vulgaris (1971 DATA)

Arrow widths are proportional to frequency of transition.*
Upward pointing arrows are returning to RETREAT DISPLAY.
Outward pointing arrows are leaving courtship; e.g. to breathe.

* 1 mm = 5 observations.

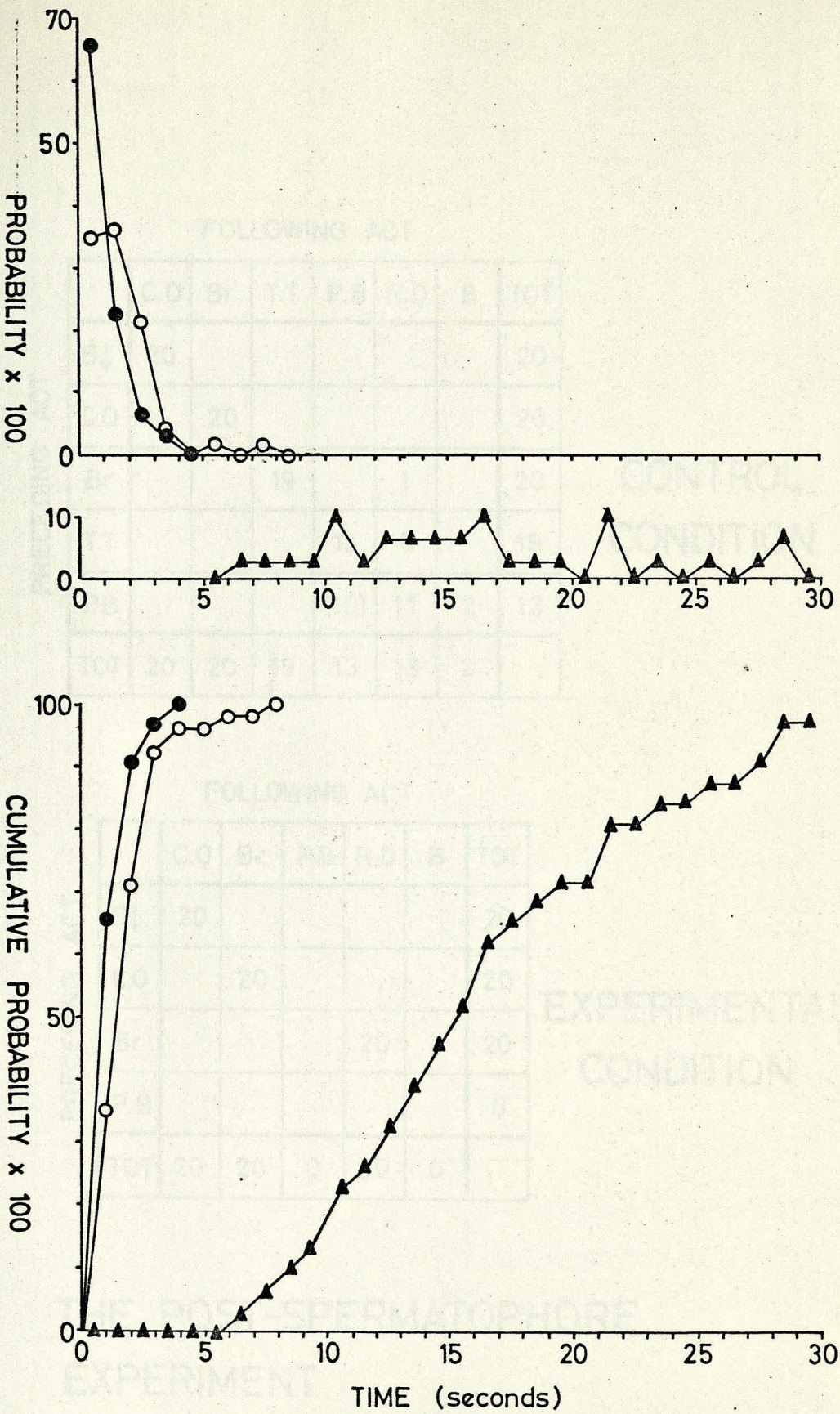
EXPT	ORDER OF TESTS	TEST CONDITIONS					
		A	B		C		
		E	C	E	C	C	E
1	A B C	+	-	+	-	-	+
2	B C A	+	-	+	-	-	+
3	C A B	+	-	+	-	-	+
4	A C B	+	-	+	-	+	
5	B A C	+	-	+	-	-	+
6	C B A	+	-	+	-	+	
7	A B C	+	-	+	-	-	-
8	B C A	+	-	+	-	-	+
9	C A B	+	+		-	-	+
10	A C B	+	-	+	-	-	+
11	B A C	+	-	+	+		
12	C B A	+	-	+	-	-	+
TAIL-TOUCH GIVEN:		12	0	11	0	0	9
SPERMATOPHORE DEPOSITED		12	1	11	1	2	8

OVERALL RESULTS		SPERMATOPHORE DEPOSITED	
		+	-
TAIL-TOUCH GIVEN:	+	31	1
	-	4	31

THE TAIL-TOUCH EXPERIMENT

E: Experimental condition. C: Control condition.

+: Spermatophore deposited. -: Spermatophore not deposited.



TRANSITIONS AFTER QUIVER

○—○ QUIVER to ♀ TAIL-TOUCH; 1971 Observational data (N = 52).
●—● QUIVER to ♀ TAIL-TOUCH; Experimental data (N = 32).

▲—▲ QUIVER to ♂ TURN BACK; Experimental data (N = 32).

For raw data see Appendix 3 m.

FOLLOWING ACT

PRECEDING ACT	C.O	Br	T.T	P.B	R.D	B	TOT
S↓	20						20
C.O		20					20
Br			19		1		20
T.T				13	6		19
P.B				(10)	11	2	13
TOT	20	20	19	13	18	2	

CONTROL CONDITION

FOLLOWING ACT

PRECEDING ACT	C.O	Br	P.B	R.D	B	TOT
S↓	20					20
C.O		20				20
Br				20		20
P.B						0
TOT	20	20	0	20	0	

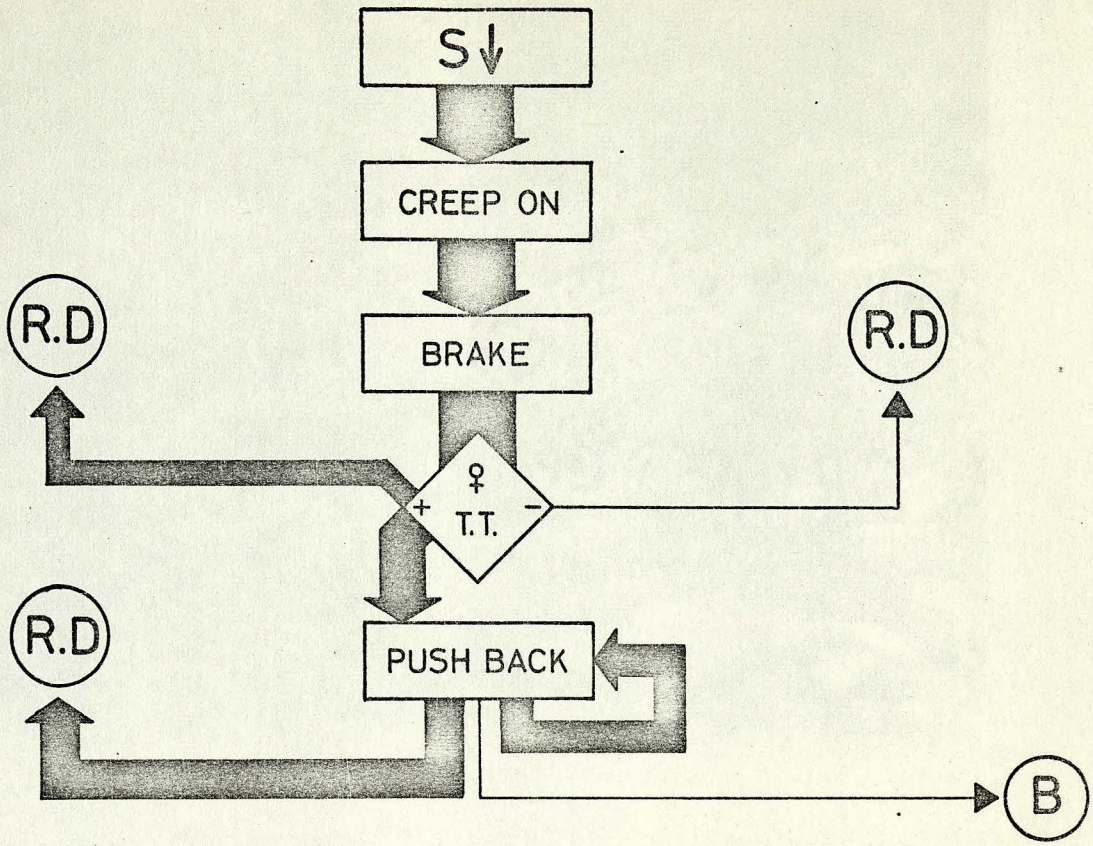
EXPERIMENTAL CONDITION

THE POST-SPERMATOPHORE EXPERIMENT

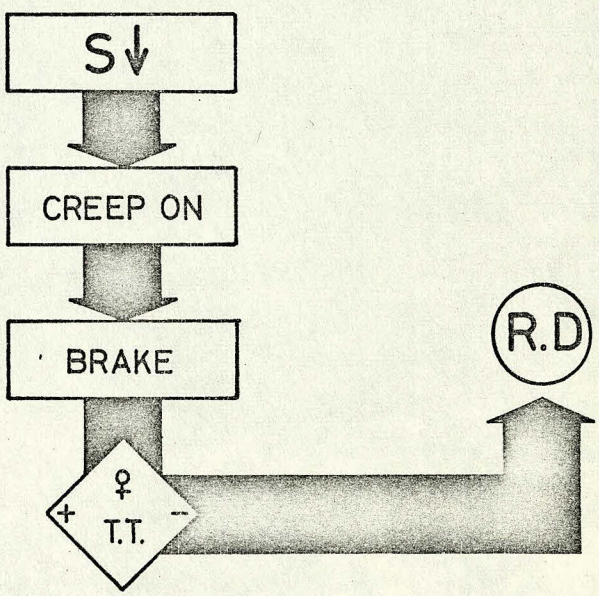
TRANSITION MATRICES

ABBREVIATIONS: S : Spermatophore deposition; C.O: Creep-On; Br: Brake; T.T: Tail-Touch; P.B: Push Back; R.D: Retreat Display; B: Breathe; TOT: Totals.

A



B



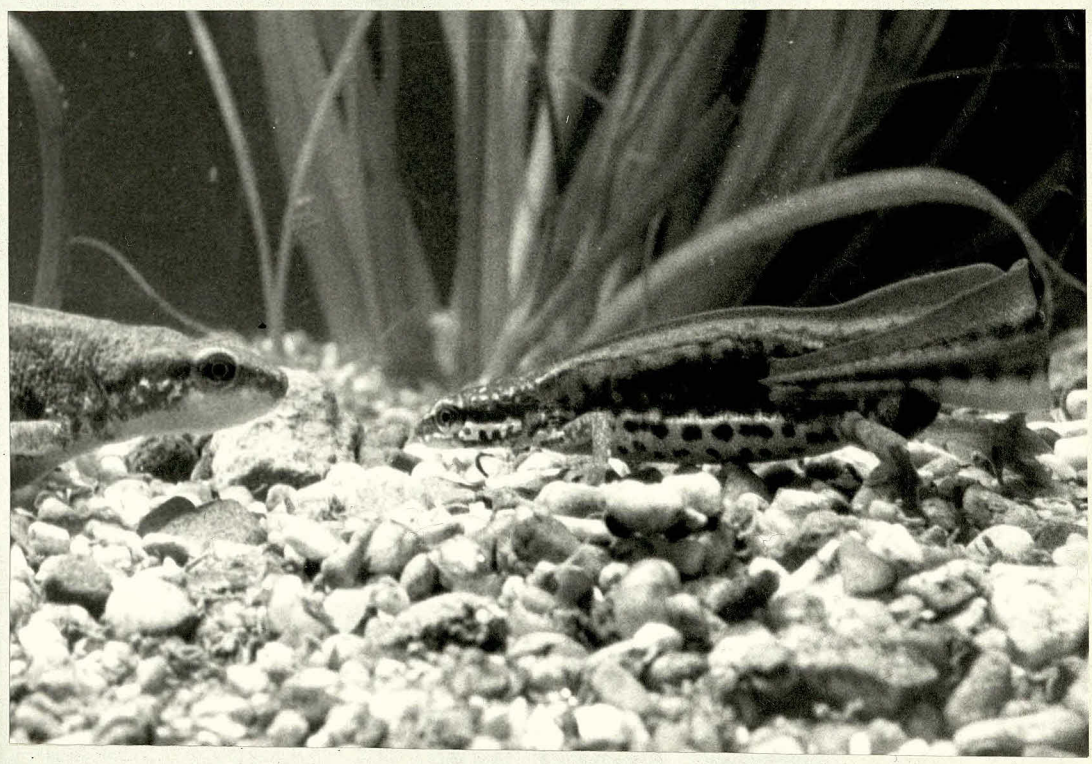
THE POST-SPERMATOPHORE EXPT.

A: CONTROL CONDITION. B: EXPERIMENTAL CONDITION.

Arrow widths are proportional to frequency of transition: 1mm = 2 observations.

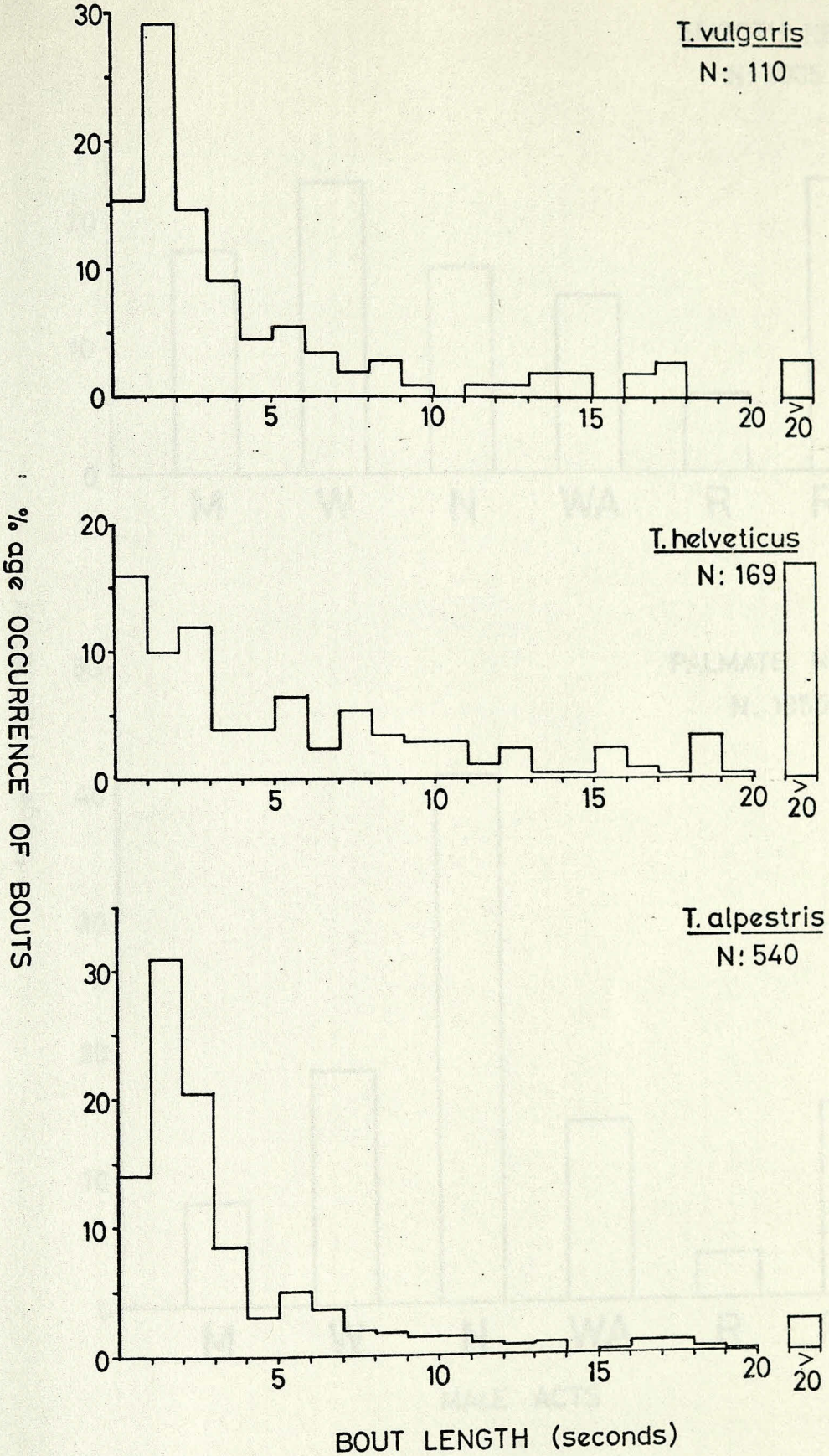
R.D: Retreat Display. B: Breathe. T.T: Touch Tail.





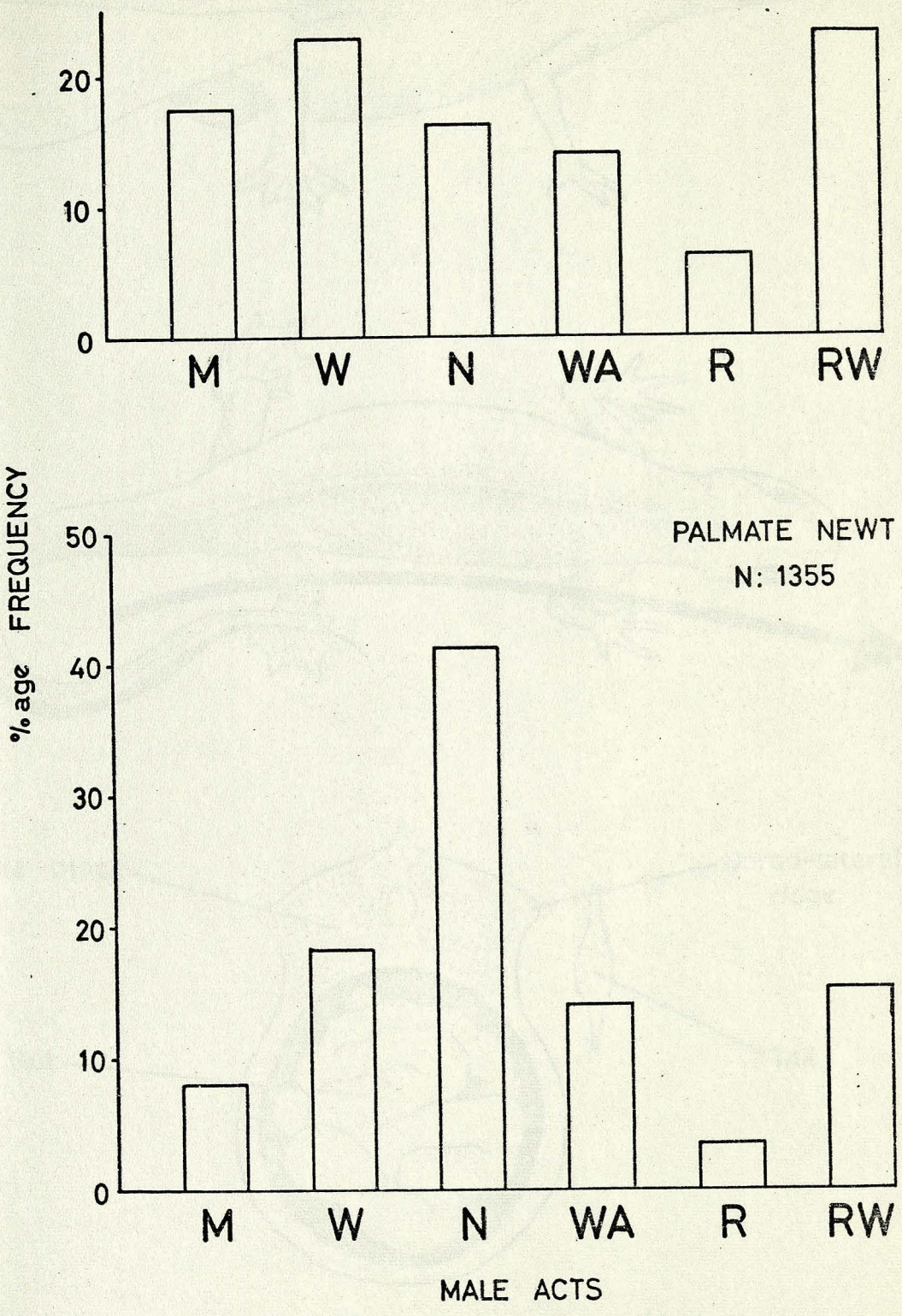
COURTSHIP IN PALMATE NEWT:

FANNING



DURATION OF UNINTERRUPTED FANNING BOUTS (1971 data)

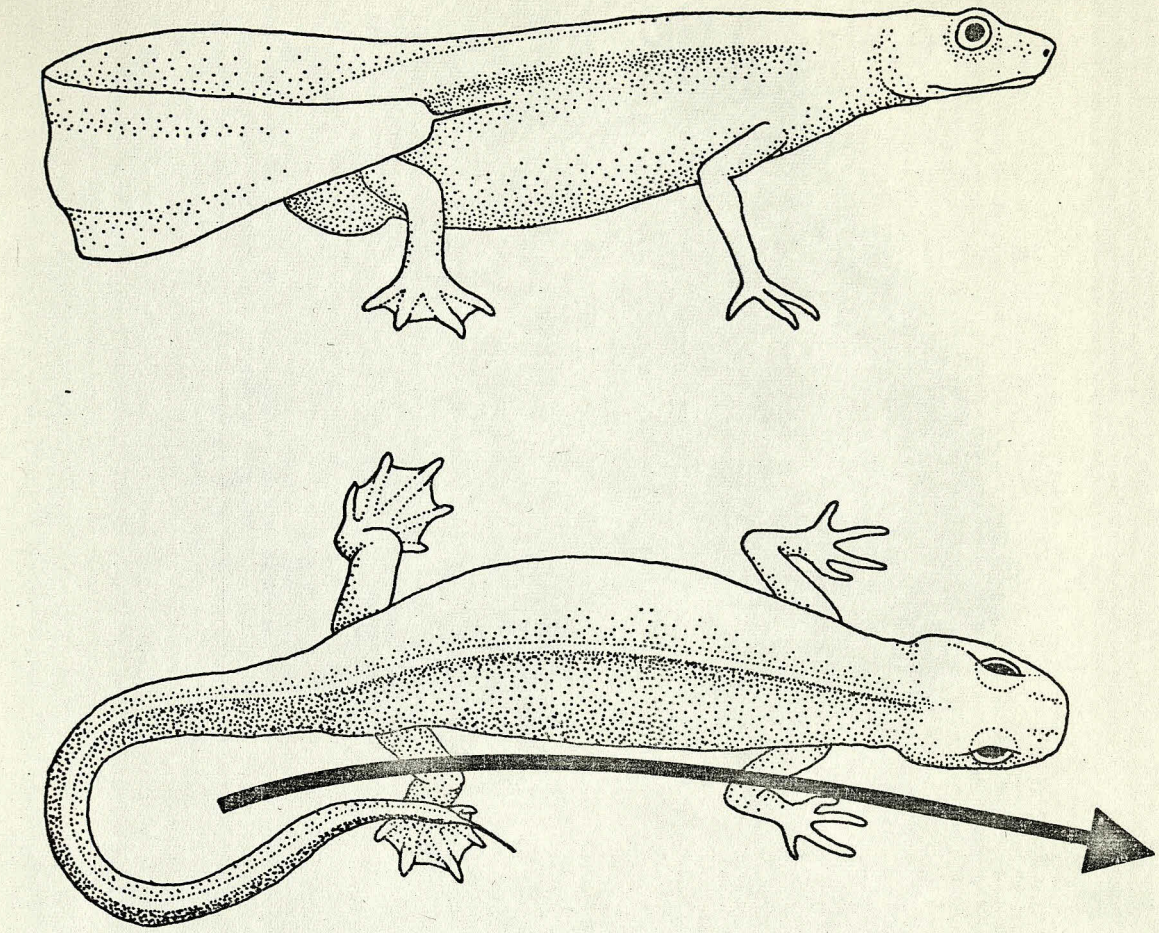
For raw data and statistical comparisons see Appendix 4 a.

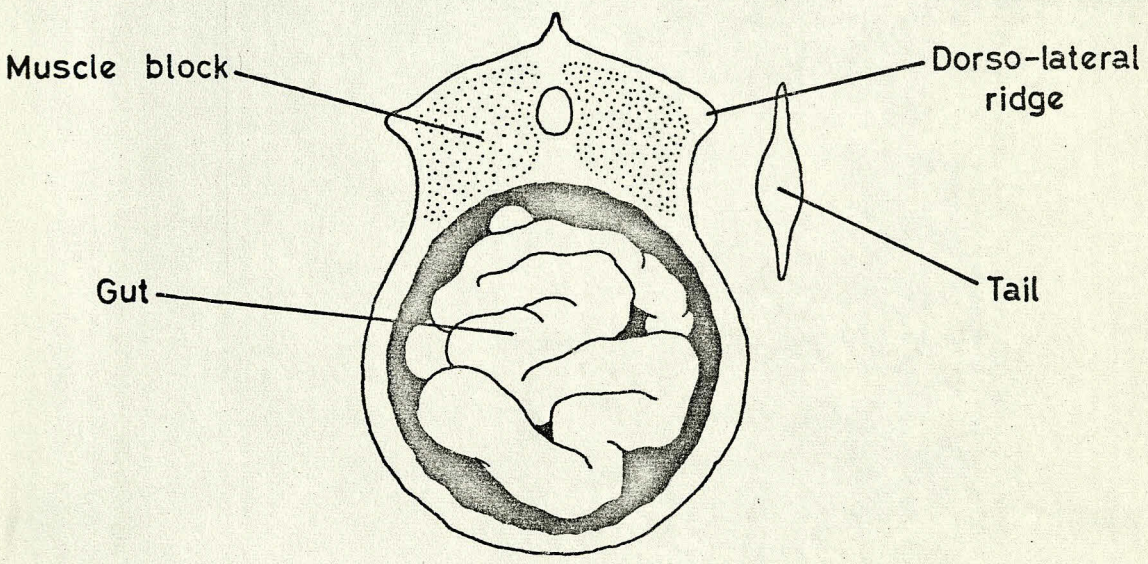


COURTSHIP OF SMOOTH AND PALMATE NEWTS:

RELATIVE FREQUENCIES OF ♂ DISPLAY ACTS

For raw data see Appendix 4b.

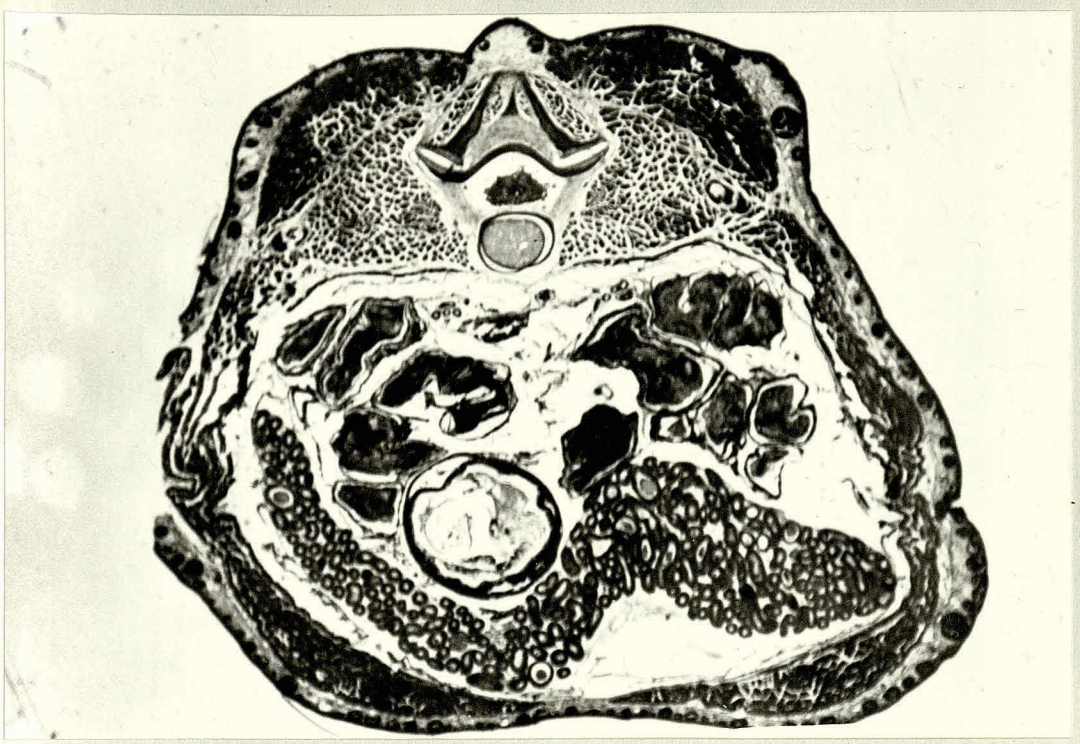


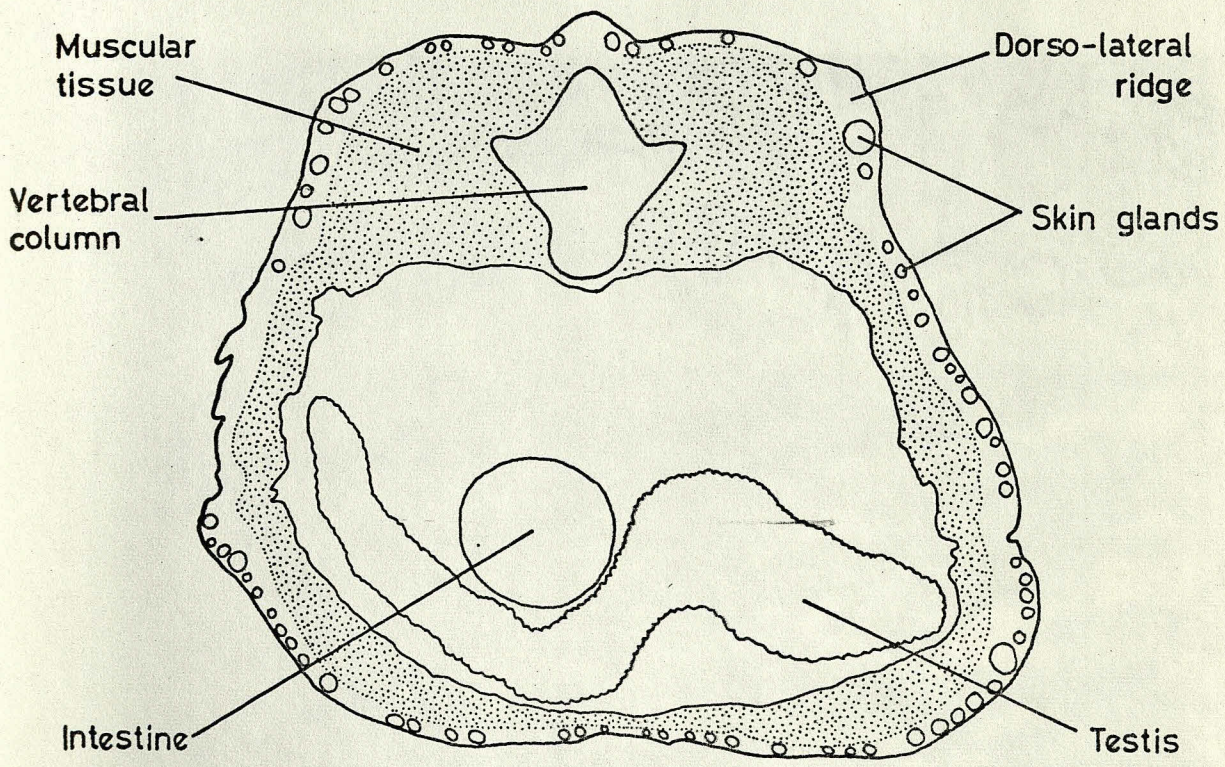


TRANSVERSE SECTION

COURTSHIP OF PALMATE NEWT:

FANNING AND THE LATERAL GROOVE





PALMATE NEWT: TRANSVERSE SECTION

Transverse section of male Palmate Newt, Triturus helveticus, in breeding condition (x 16).

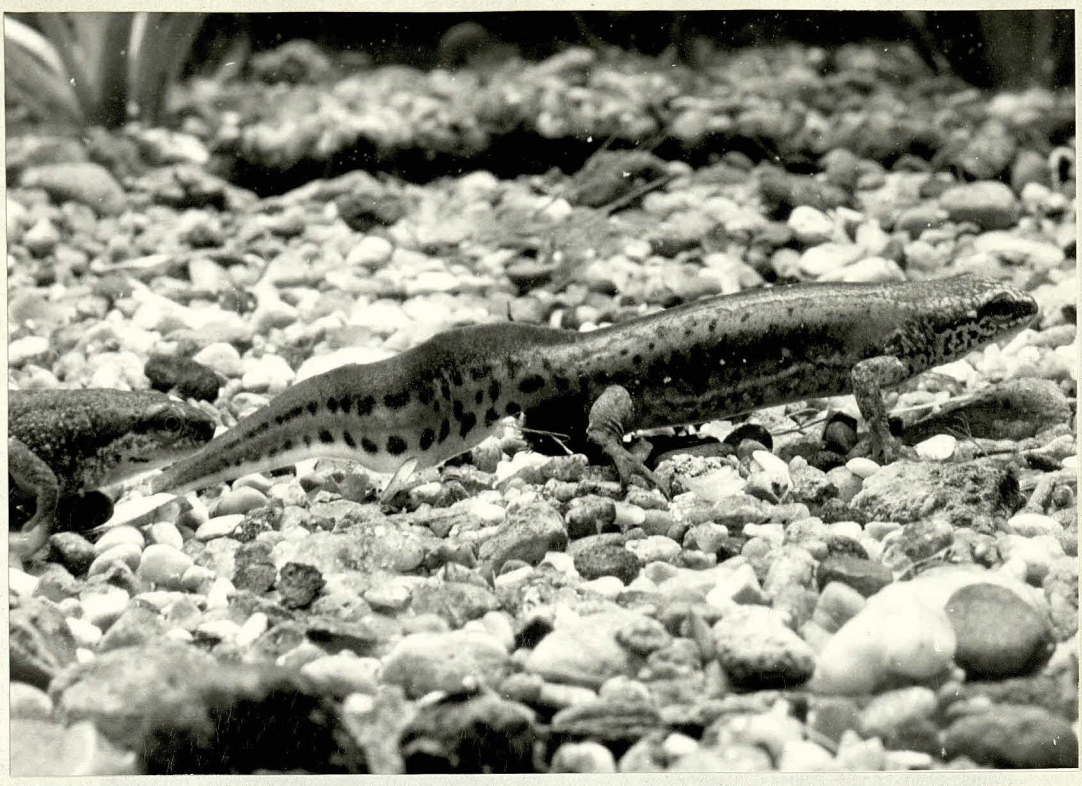


FIG A: The male QUIVERS; the female is about to TAIL-TOUCH.

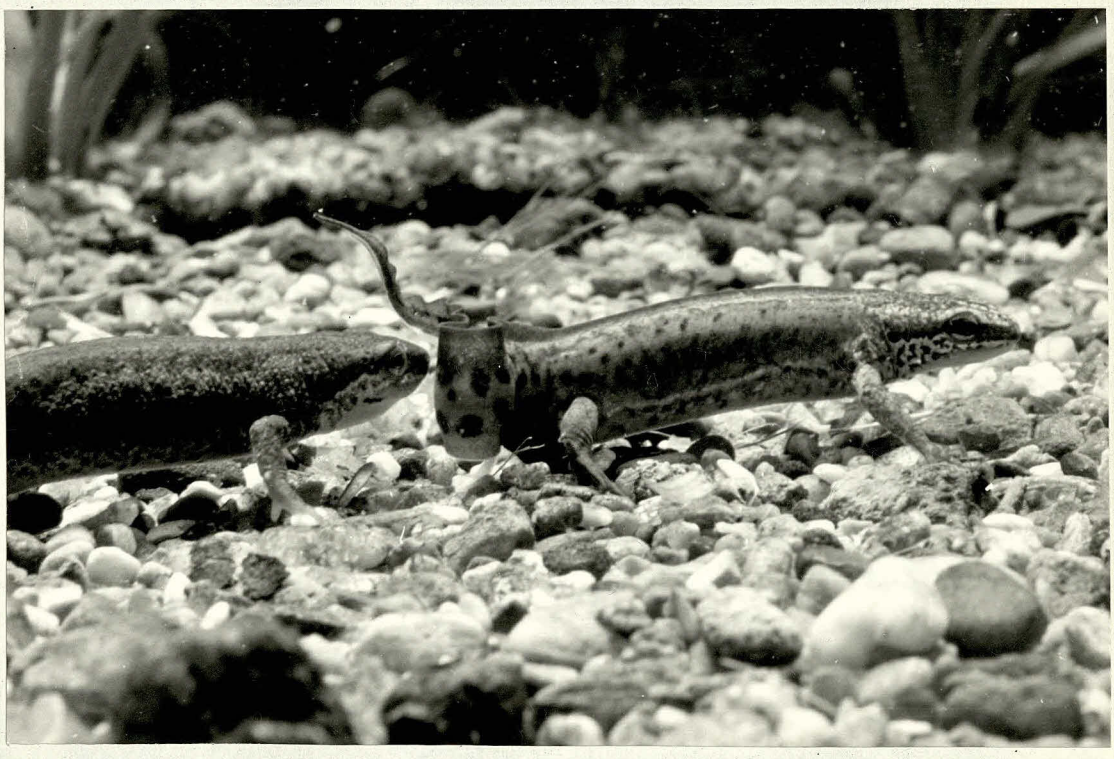


FIG B: The TAIL-TOUCH has been given; the male is about to deposit a spermatophore.

COURTSHIP OF PALMATE NEWT:

DEPOSITION PHASE 1.



FIG A: Deposition of Spermatophore.



FIG B: CREEP-ON.

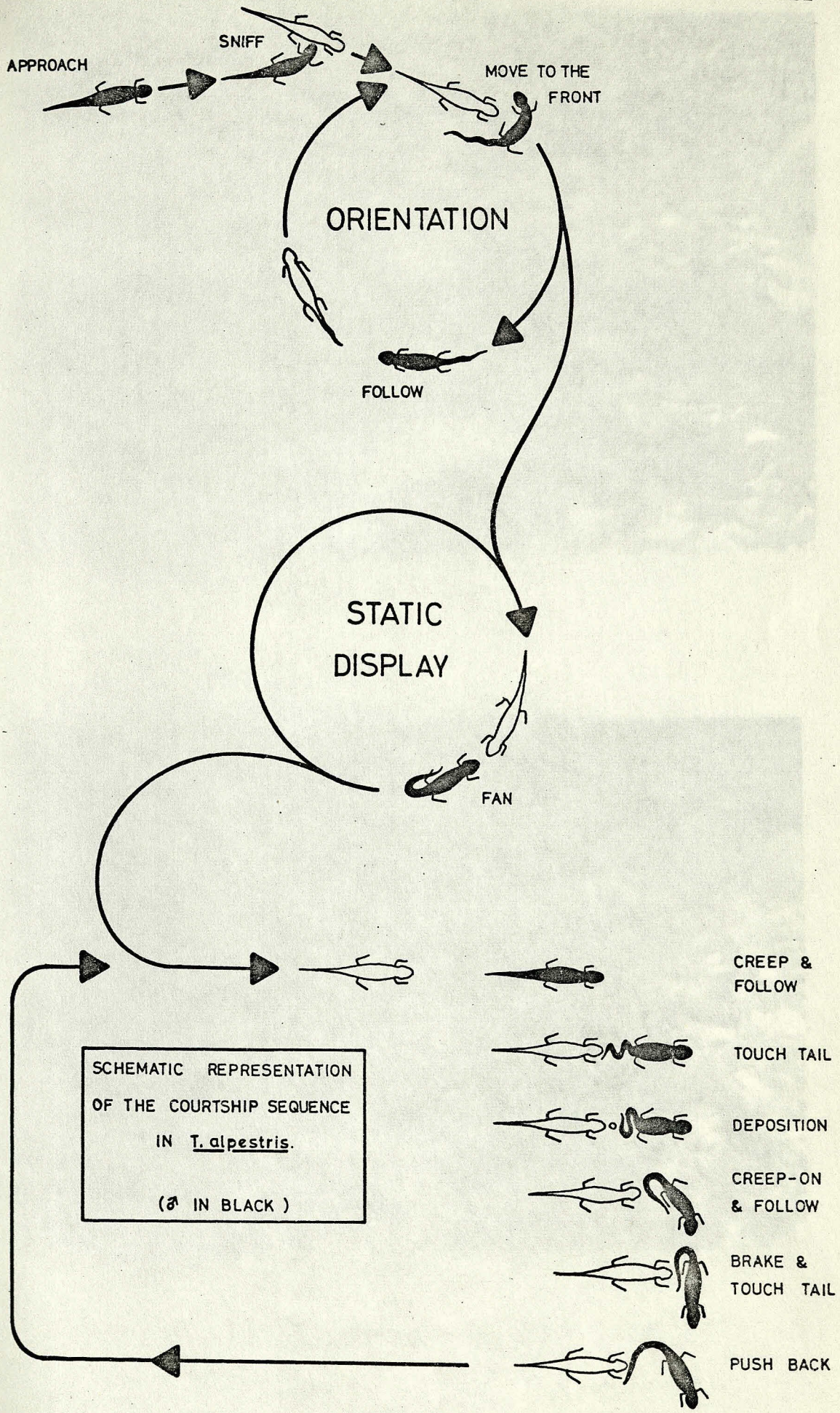


FIG C: BRAKING.

COURTSHIP OF PALMATE NEWT:

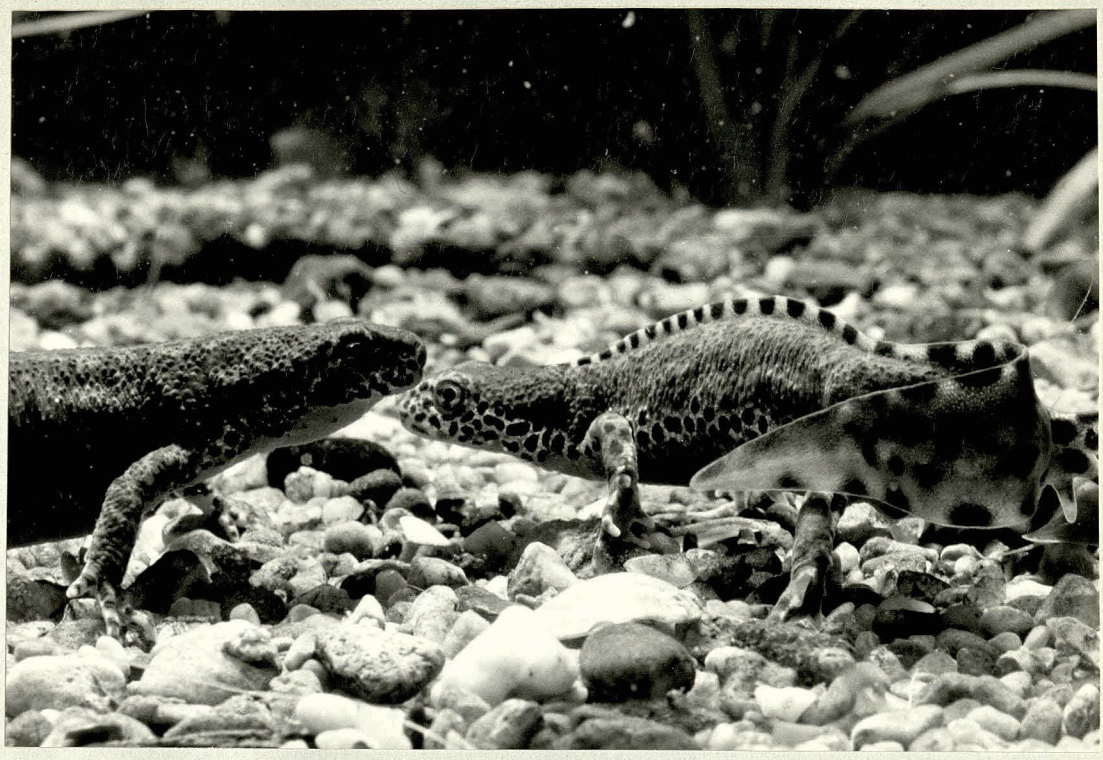
DEPOSITION PHASE 2.

(Note the position of the newts relative to the Snail on the right.)



SCHEMATIC REPRESENTATION OF THE COURTSHIP SEQUENCE IN T. alpestris.

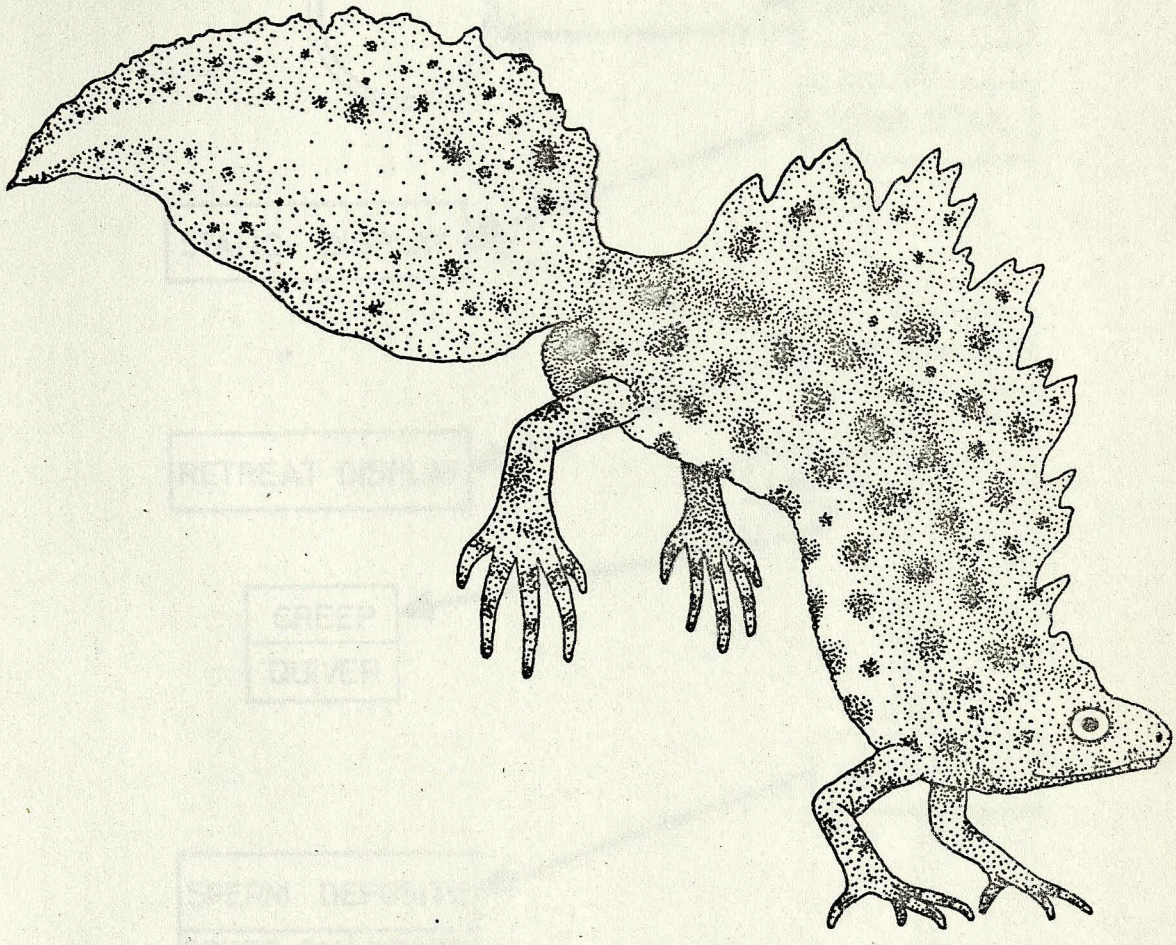
(♂ IN BLACK)





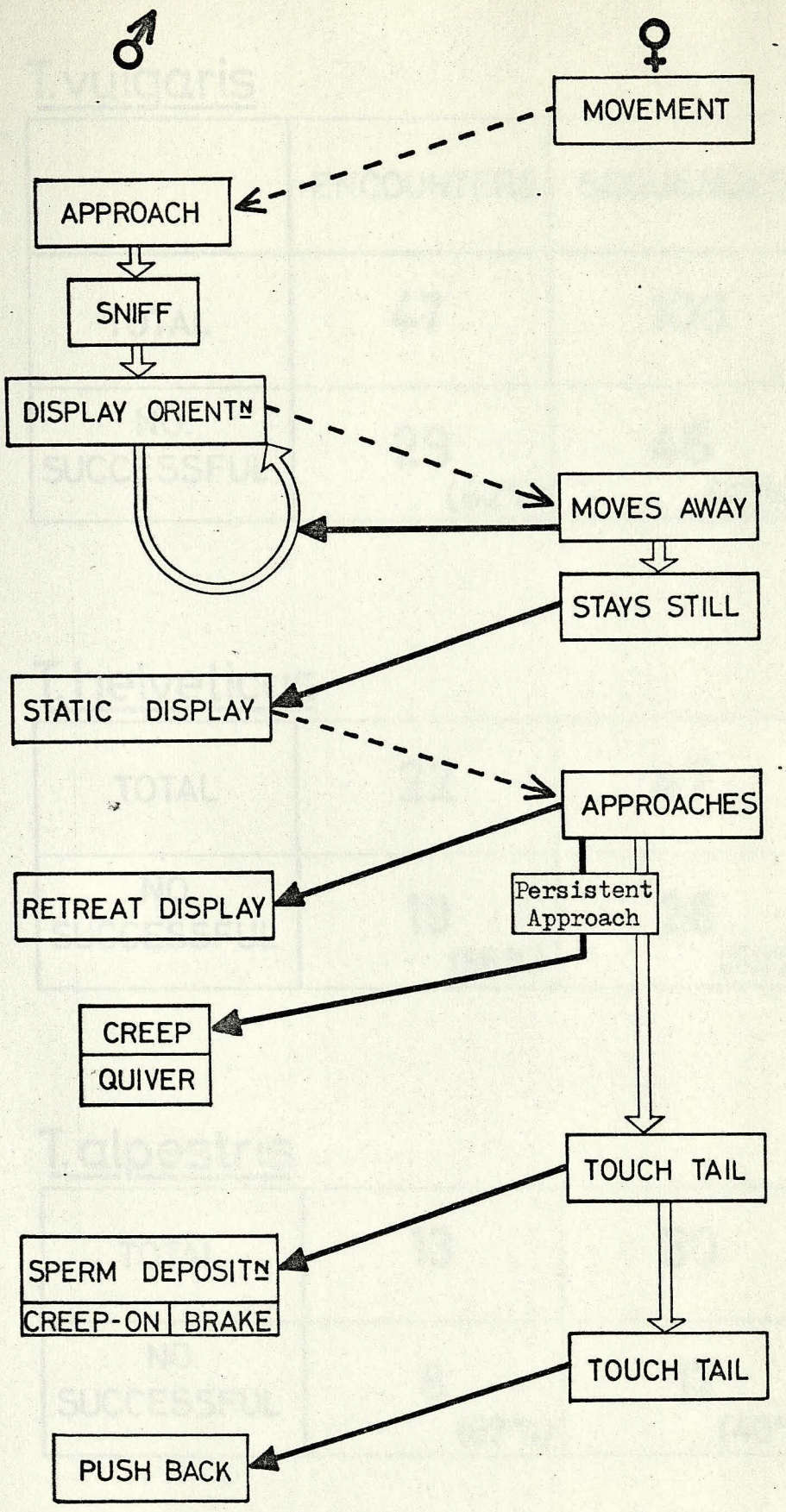
COURTSHIP OF ALPINE NEWT:

FANNING



COURTSHIP OF CRESTED NEWT, Triturus cristatus.

THE ♂ DISPLAY POSTURE



THE NEWT COURTSHIP SEQUENCE AS A STIMULUS-RESPONSE CHAIN (T. vulgaris and T. helveticus)

T. vulgaris

	ENCOUNTERS	SEQUENCES
TOTAL	47	106
NO. SUCCESSFUL	29 (62%)	46 (43%)

T. helveticus

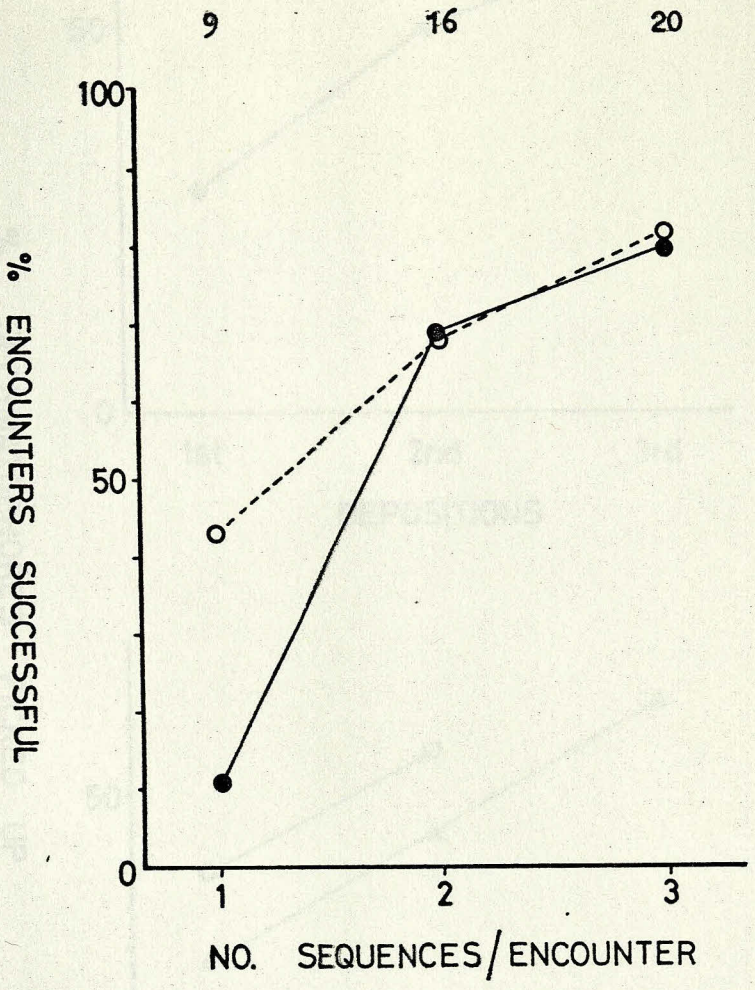
TOTAL	22	47
NO. SUCCESSFUL	19 (86%)	28 (60%)

T. alpestris

TOTAL	13	30
NO. SUCCESSFUL	8 (62%)	12 (40%)

OVERALL SUCCESS OF ENCOUNTERS & SEQUENCES

Figures for Encounters include only those in which there were completed Sequences (i.e: at least one Spermatophore was deposited).



ENCOUNTER SUCCESS

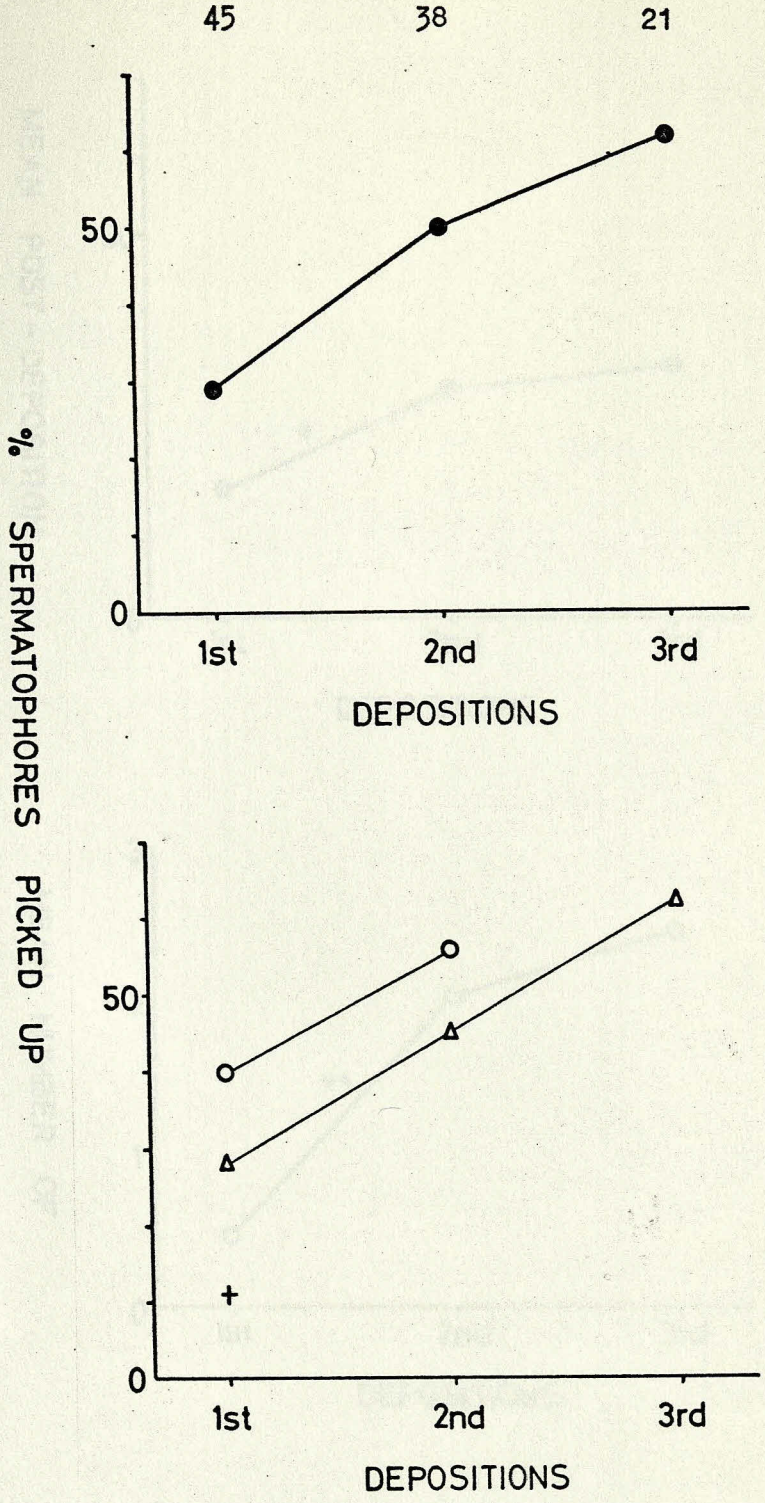
T. vulgaris

●——● Observed values.

o---o Values expected on the basis of a uniform Sequence success rate.

Figures at the top indicate the number of observations on which each point is based.

For raw data see Appendix 4 c.



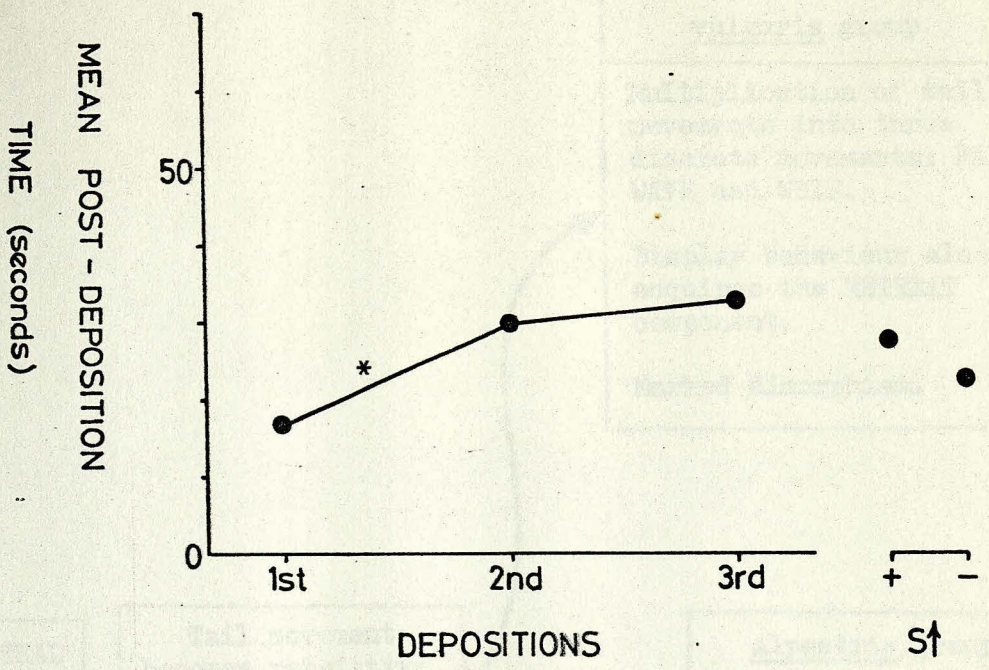
SEQUENCE SUCCESS

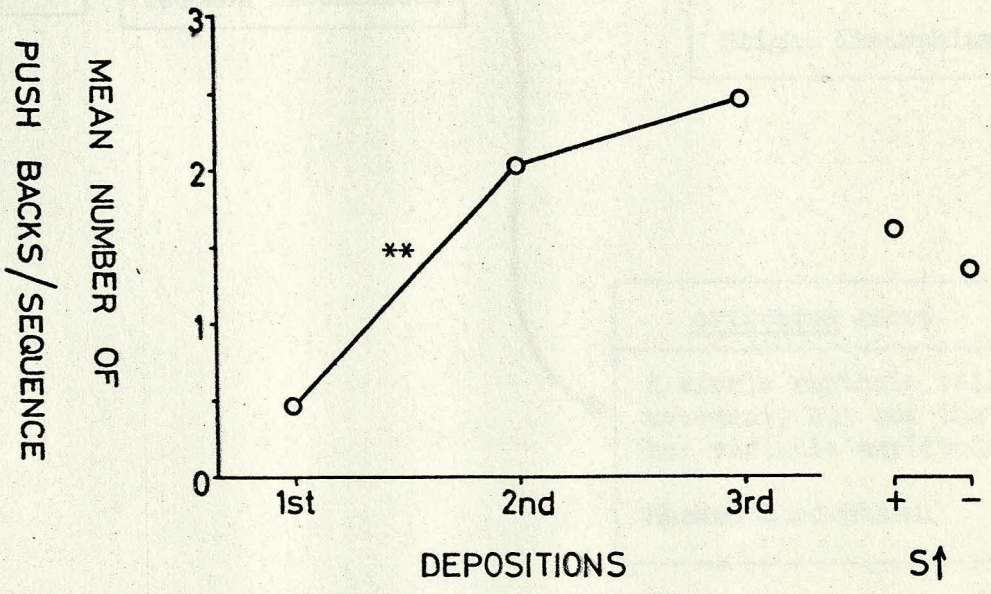
T. vulgaris

●——● Combined data for all Encounters. Figures at top indicate the number of observations on which each point is based.

\+ Data from Encounters incorporating 1 Sequence.
o——o Data from Encounters incorporating 2 Sequences.
Δ——Δ Data from Encounters incorporating 3 Sequences.

For raw data see Appendix 4 c.





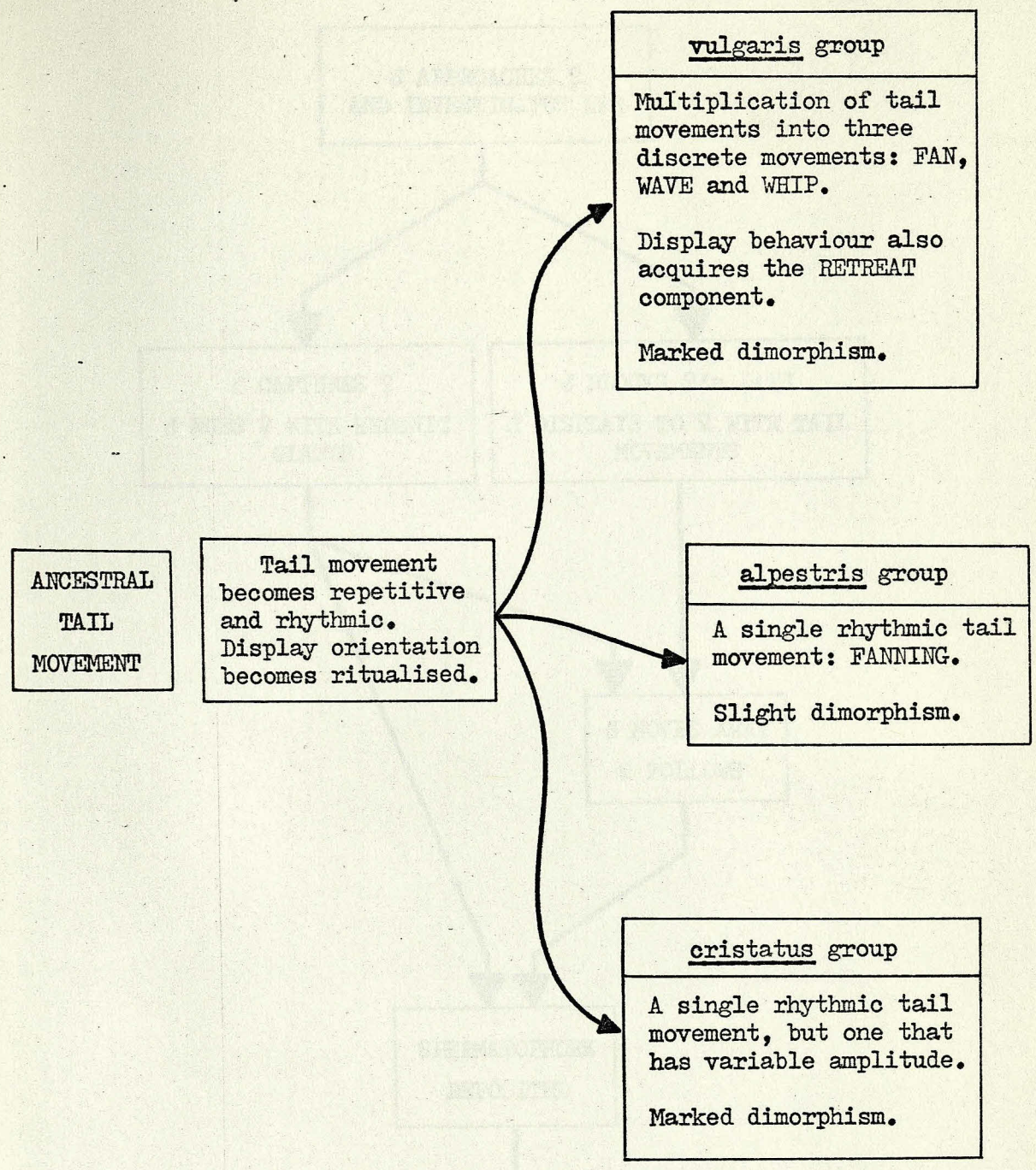
CORRELATES OF SEQUENCE ORDER. T. vulgaris

* Scores for 1st and 2nd Sequences are significantly different: p 0.01 (Mann-Whitney U Test).

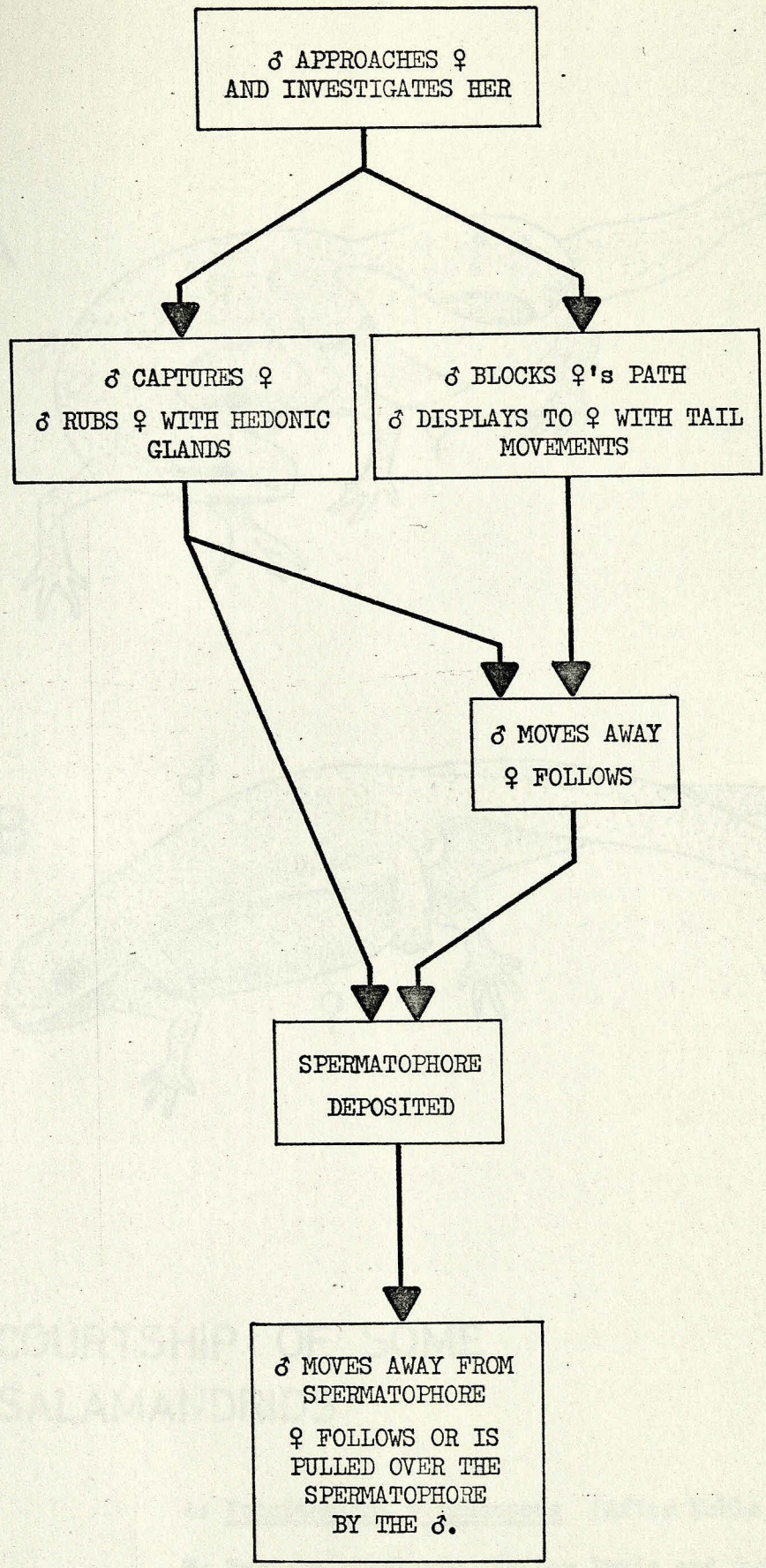
** Scores for 1st and 2nd Sequences are significantly different: p 0.001 (Median Test).

On the right of each graph are shown scores for Successful (+) and Unsuccessful (-) Sequences.

For raw data see Appendix 4 c.

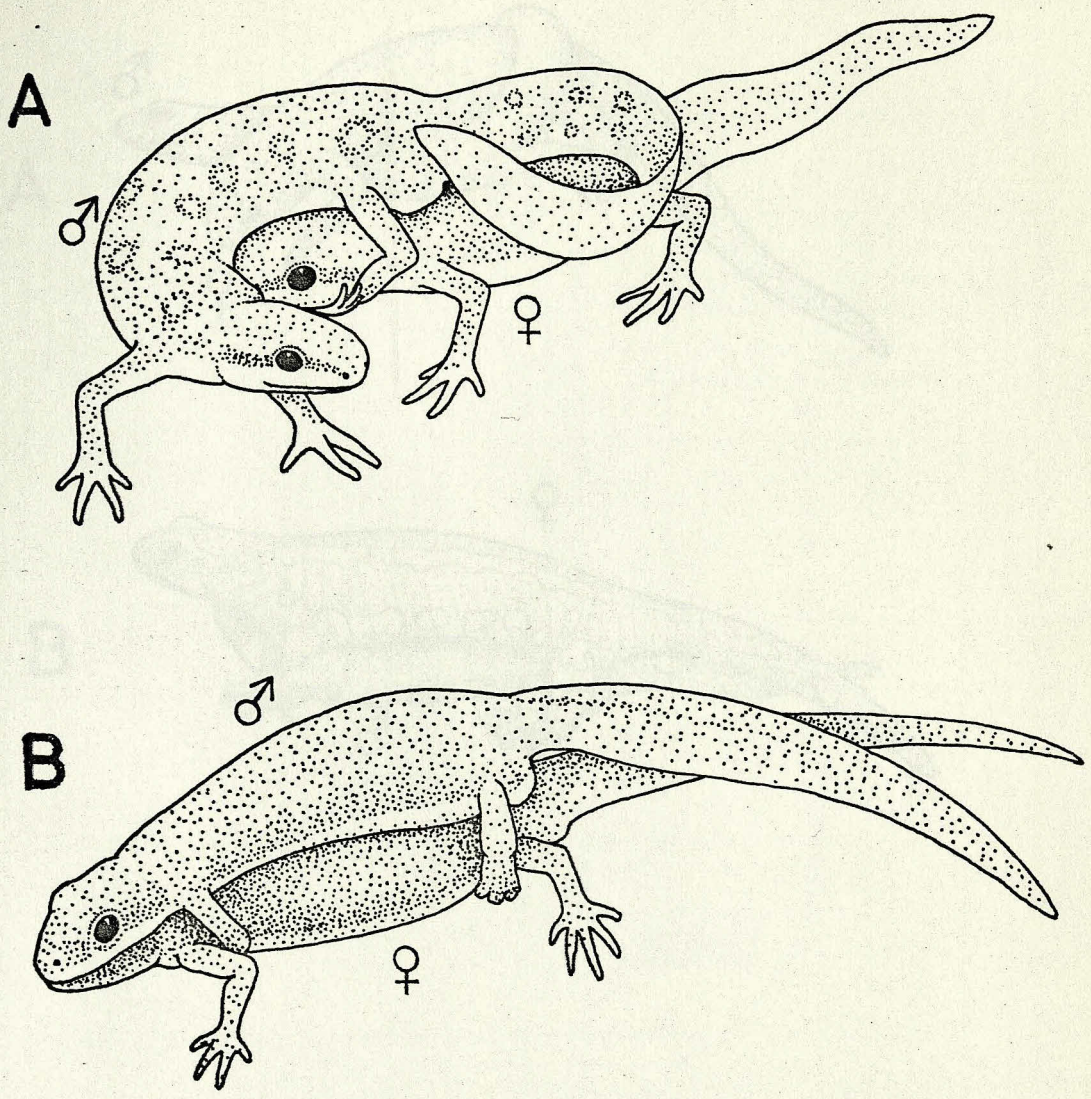


EVOLUTION OF Triturus SEXUAL BEHAVIOUR



SEXUAL BEHAVIOUR OF URODELES

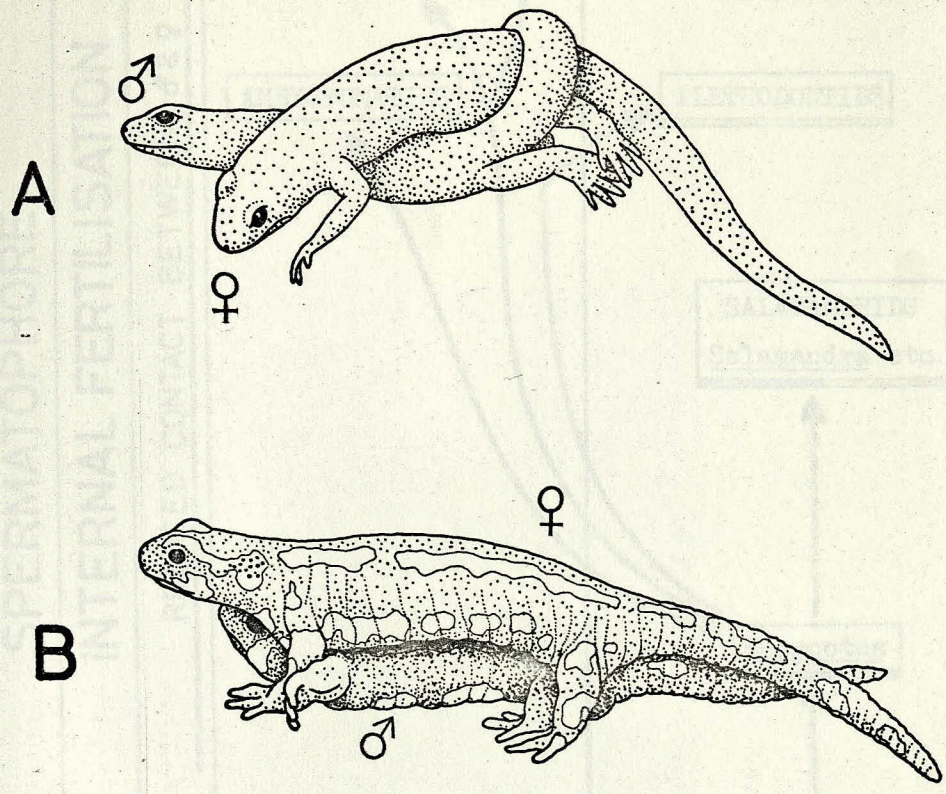
(After Salthe 1967)



COURTSHIP OF SOME SALAMANDRIDS

A: Notopthalmus viridescens (After Noble 1931).

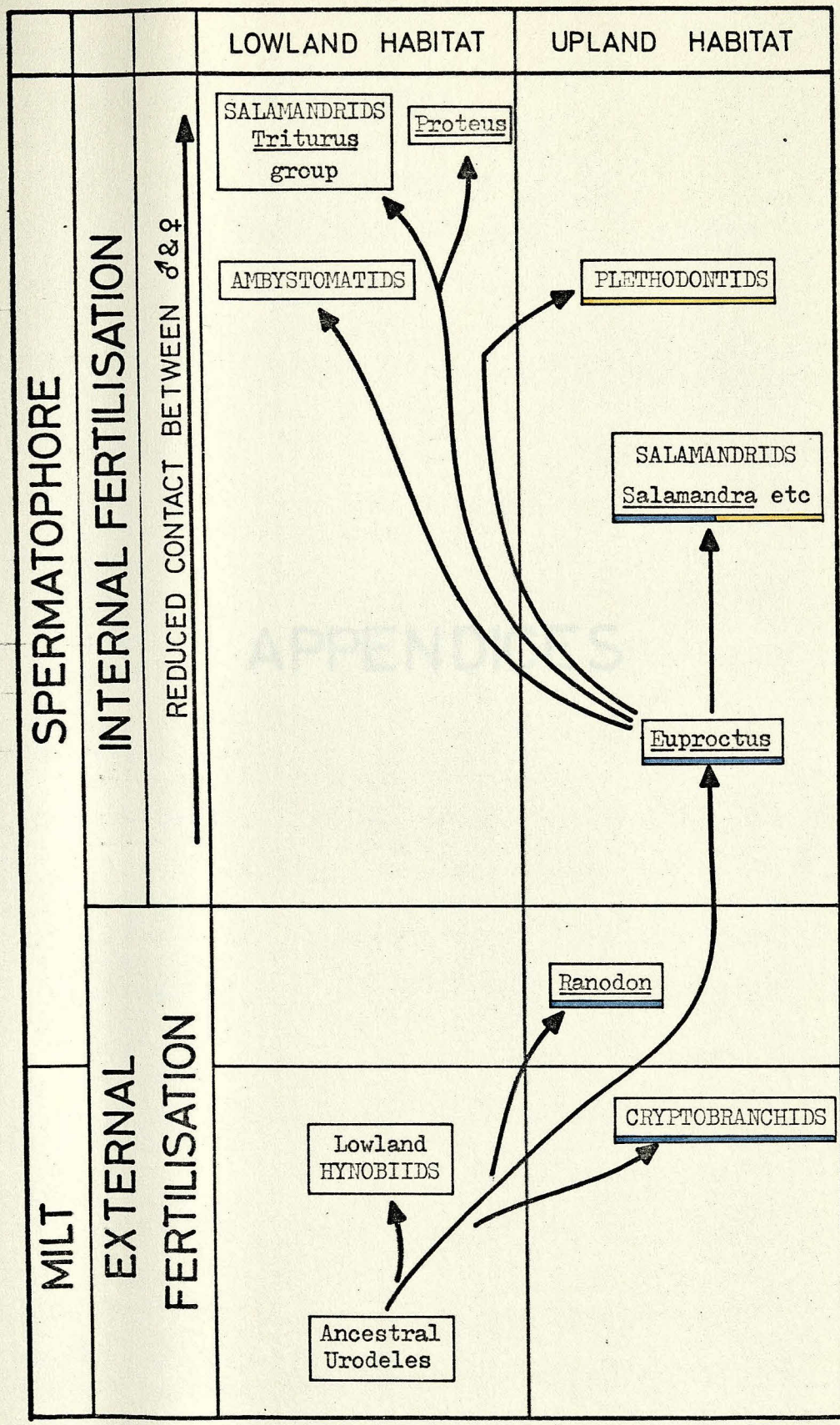
B: Taricha rivularis (After Davis and Twitty 1964).



COURTSHIP OF SOME SALAMANDRIDS

A: Euproctus asper (After Ahrenfeldt 1960).

B: Salamandra salamandra (After Joly 1966).



EVOLUTION OF SEXUAL BEHAVIOUR OF URODELES

Mating in running water. Terrestrial mating.

After Salthe (1967).

APPENDICES

APPENDIX 1

OBSERVATIONAL DATA

Number of Animals Used

SPECIES	vulgaris			helveticus		alpestris	
YEAR	1970	1971	1972	1970	1971	1971	1972
TOTAL ENCOUNTERS	40	43	52	21	31	22	14
TOTAL SEQUENCES	55	51	74	19	28	35	9
Unconsummated Encounters *	18	18	21	10	20	8	8
Total ♂♂ used	10	24	24	6	14	5	8
Total ♀♀ used	13	24	15	5	14	4	8
♂♂ used more than once	9	8	15	2	5	4	3
♀♀ used more than once	5	10	12	4	8	3	4
♂ ♀ combinations used more than once	5	2	9	5	2	7	2
Maximum number of times same ♂ used	15	5	6	15	8	11	4
Maximum number of times same ♀ used	9	5	15	9	5	11	4
Maximum number of times same pair used	4	2	3	7	2	6	2

* Unconsummated Encounters are those in which no Spermatophores were deposited.

APPENDIX 2 a

A Comparison of Behavioural Terms used in this Thesis with those of previous Authors.

A + indicates that a behaviour is described but is not given a definite name.

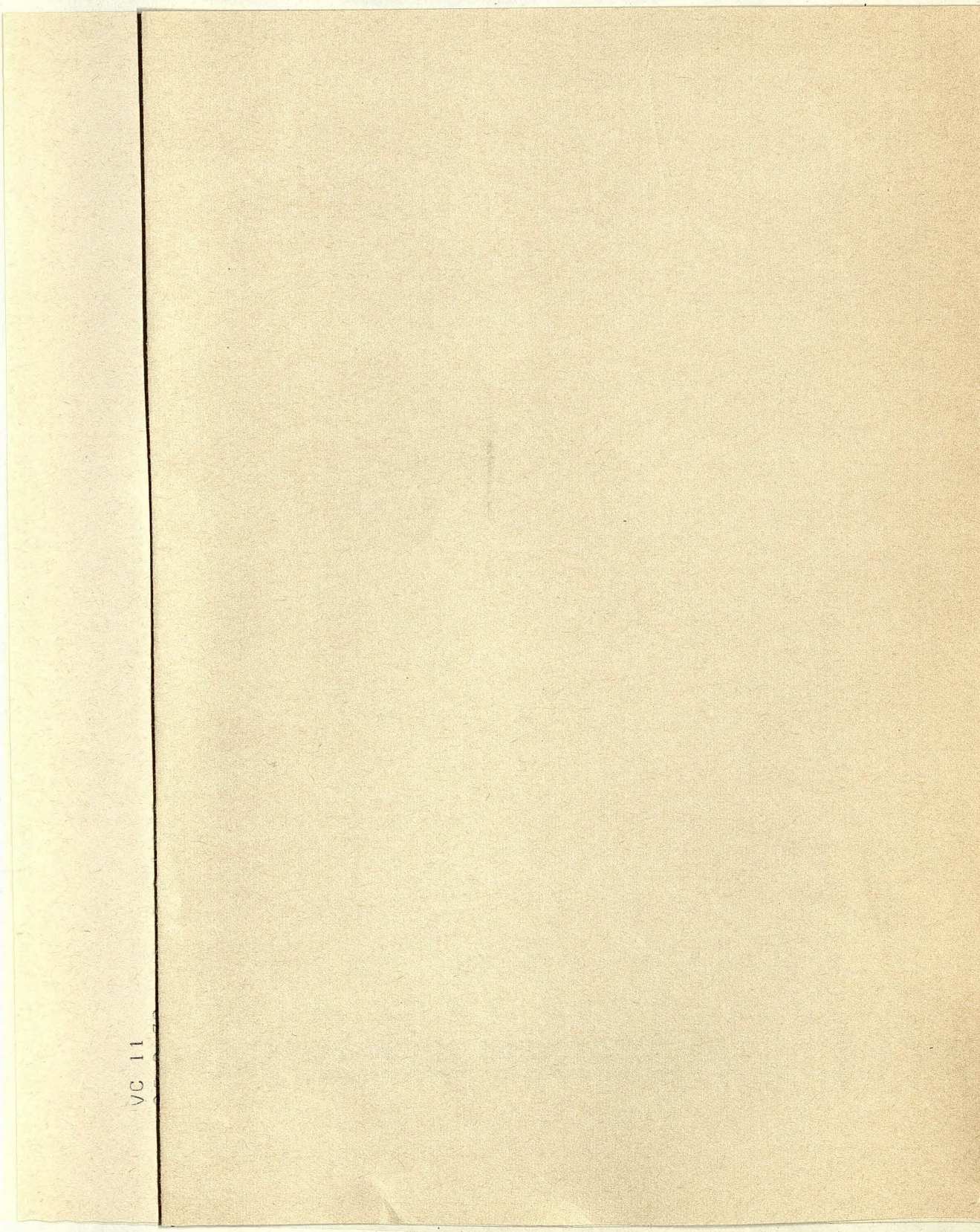
Present Description	Tinbergen and Ter Pelkwijk 1938	Prechtl 1951	Marquenie 1950
ALERT POSTURE			+
APPROACH	+	+	+
SNIFF	+	+	+
MOVE-TO-THE-FRONT	+		Jump (Sprong)
WAVE			+
WHIP	+		Whipping
FAN	Fanning ("Odour Serenade")	Tail-wagging	Fanning
TURN-ABOUT			
RETREAT-AND-WHIP			+
CREEP	+	+	Leading (Leiden)
QUIVER			+
TOUCH-TAIL			+
CREEP-ON			+
BRAKE			Braking
PUSH-BACK			

APPENDIX 2 b

The Organ Record of a typical sexual encounter, in which three spermatophores were deposited.

Symbols are as in the Glossary (page 1/42) with the addition of:
XX = ♀ move away. XA = ♀ approach ♂.

The gaps in the record represent losses of contact between ♂ and ♀.



```
VC 11
28 2 72
M 11  F 21
T 19 5



   27 A
   62 A
  109 SN
  213      XX
  304 A
  447      XX
  460      XX
  471      XX
  480 -T


   18 A
   29 SN
   61 SN
  136      XX
  167 F
  219      XX
  330 SN
  387 M
  392 W
  615      XX
  780      XX
  886 A
 1054      XX
 1061 -T


   29 A
   43      XX
   49 F
   56      XX
   61 F
   67      XX
   73 F
  106 M
  110 W
  171      XX
  177 F
  183      XX
  189 F
  195 M
  198 W
  221      XA
  228 RW
  248      XA
  259 RW
  287 W
  299      XA
  307 RW
  324      XA
  331 R
  336      XA
  342 RW
  365      XA
  384 WA
  392 RW
  402      XA
  422 C
  434      XA
  446 Q
  456      TT
  475 S
  516 CO
  522      XA
  541 BR
  607 A
  630 RW
  642      XA
  648 RW
  655      XA
  667 RW
  673      XA
  684 C
  691      XA
  702 Q
  709      TT
  726 S
  747 CO
  763      XA
  780 BR
  798      TT
  809      SU
  840 PB
  880 PB
  897 RW
  913      XA
  926 RW
  938      XA
  951 RW
  965      XA
  988 R
  996      XA
 1002 RW
 1007      XA
 1012 RW
 1018      XA
 1027 RW
 1032      XA
 1067 R
 1074      XA
 1084 C
 1092      XA
 1099 Q
 1107      TT
 1141 S
 1160 CO
 1189      XA
 1200 BR
 1213      TT
 1377      XG
 1407 -T

END
```

APPENDIX 3 a

MALE APPROACHES

DISTANCE (cm)	0 - 5	5 -10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	TOTAL
1st APPROACHES	40	8	2	1				1		52
SUBSEQUENT APPROACHES	51	22	10	9	1	2			1	96
ALL APPROACHES	91	30	12	10	1	2		1	1	148

Comparison between first and subsequent Approaches:

$D = 0.2380$

$0.01 < p < 0.05$

(Kolmogorov - Smirnov Test)

APPENDIX 3 b

Fisher Exact Tests for Results of Approach Experiment:

8	2
2	8

p = 0.011

8	2
0	10

p = 0.0004

APPENDIX 3 c

DISTRIBUTION OF MALE SNIFFING BOUTS

YEAR	Number of Sniffing Bouts directed at different parts of ♀'s body.				
	TAIL	CLOACA	TRUNK	HEAD	TOTAL
1970	14	65	43	10	132
1971	63	82	119	25	289
1972	69	49	90	17	225
MARQUENIE DATA (1950)	82	139	32	20	273

Statistical treatment of 1970, 1971 and 1972 data - 3 x 4 chi-square.

Chi-square for 6 d.f. = 38.35.

$p < 0.001$.

APPENDIX 3 d

Frequency distributions of time intervals between consecutive acts.

1971 Data

1st ACT	2nd ACT	½ sec time intervals after 1st act												> 12	TOT
		1	2	3	4	5	6	7	8	9	10	11	12		
M	W	149	90	8	1	2									250
W	W		7	1	2	3		1	3	1			1		19
	N	2	30	41	21	22	16	6	3	1	2	1		2	147
	WA		1	2		2	5	1	2	3	2	1		1	20
	♀ -	3	19	15	20	18	10	9	8	3	4	5	3	13	130
	♀ +	1	17	10	9	12	5	5	4	4	3	2	2	14	88
Ns	Ne	2	15	22	12	8	8	7	5	1	4	4	2	24	114
	♀ -	1	3	2	6	15	8	8	9	3	3	3		17	78
	♀ +	12	23	14	4	3	5	2	4	2	1			6	76
Ne	RW	2	10	14	4	2	1	1						1	35
	WA	2		5	2	4	2	4	2		3	1		9	34
	♀ -	1	17	21	9	10	10	1				3	1	6	79
	♀ +	1	7	7	7	4	6	1	2	3	1	2	1	9	51
WA	W		8	3	2	3	4	1	1	2			1	6	31
	WA	1	4	4	2	8	2	5		3				3	32
	♀ +	9	73	6	7	5	1	2						4	107
RW	N		2	4	6	9	2	5	1						29
	WA	1	1	1	1	2	3	2	1		1			10	23
	♀ +	49	117	57	39	22	12	5	5	4		1	1	2	314
R	♀ +	15	50	5	3	1			1		1			1	77
♀ -	A		3	2	1	1	4	1			2	1	2	10	27
	F	244	393	109	46	29	15	7	5	8	6	2	1	14	879
	M	1	11	4	2	4	1	3	2					2	30
	Ne	33	31	5	4			1	2					2	78
♀ +	W	3	17	15	9	8	4	5	1	1		1		1	65
	Ns	1	10	12	9	4	2	6	2						46
	Ne	30	25	6	8		1	3		2				1	76
	WA		5	6	13	10	9	4	5	3	4		2		61
	R		13	14	6	14	10	4	2	4	2			4	73
	RW	15	75	84	51	44	20	16	3	2	4	1	2	4	321
	C	2	42	19	12	11	1	1	1		1	2	1		93

APPENDIX 3 d

Frequency distributions of time intervals between consecutive acts.

1972 Data

1st ACT	2nd ACT	½ sec time intervals after 1st act												> 12	TOT
		1	2	3	4	5	6	7	8	9	10	11	12		
M	W	199	23	2						1					225
W	W	1		1	3	1	1	3		1				1	12
	N	1	33	54	36	14	7	10		1	2			1	159
	WA				2	4	6	1	1	2				8	24
	♀ -	4	15	25	18	13	6	6	2	5	2	2	3	12	113
	♀ +	2	3	8	10	2	5	2	1	2	2			4	41
Ns	Ne	5	10	9	8	14	12	8	12	3	1	5	6	25	128
	♀ -		6	6	16	13	7	3	4	3	1	1		11	71
	♀ +	9	10	3	5	2	2	6	1	2	2	2	2	5	51
Ne	RW	2	7	6	5	3									23
	WA			10	7	7	1	2	2	1		2	1	19	52
	♀ -	1	8	13	7	7	6	6	1		2	2	5	19	77
	♀ +			3	8	7		2	5			2	1	7	35
WA	W	5	36	17	9	7	6	5	1			1			87
	WA	1	3	6	1	6	3	6	1	3	1	1	1	4	37
	♀ +	4	31	10	8	3	2				1			1	60
RW	N		1	2	2	3	1	1			1				11
	WA				4	3	2	6	1		1	2		2	21
	♀ +	20	153	66	39	13	12	3	4	3				2	315
R	♀ +	11	57	11	3	1				1					84
♀ -	A		1		2	1	1		2			1	3	15	26
	F	159	298	81	31	19	12	8	5	5	3	4	2	10	637
	M	2	2	1	1	2		1	1	1	3			2	16
	Ne	19	47	1	3			1							71
♀ +	W	1	11	7	4	1								1	25
	Ns	2	3	4	2				1					2	14
	Ne	19	21	5	2	1	2							1	51
	WA		9	15	9	8	3	4	2	1	1			3	55
	R		13	24	14	14	4	6						3	78
	RW	11	103	94	50	18	8	5	4	1	2	1	2	3	302
	C	4	63	28	7	7	4	1	3	1	1	1		1	121

APPENDIX 3 e

Frequency distributions of time intervals between consecutive acts.

Statistical Comparison of 1971 and 1972 data.

KOLMOGOROV-SMIRNOV TEST

1st ACT	2nd ACT	D	p
M	W	0.288	***
W	W	o	
	N	0.140	n.s
	WA	o	
	♀ -	0.110	n.s
	♀ +	0.140	n.s
Ns	Ne	0.176	*
	♀ -	0.240	*
	♀ +	0.213	n.s
Ne	RW	o	
	WA	0.129	n.s
	♀ -	0.315	***
	♀ +	0.208	n.s
WA	W	0.351	**
	WA	0.103	n.s
	♀ +	0.183	n.s
RW	N	o	
	WA	o	
	♀ +	0.093	n.s
R	♀ +	0.064	n.s
♀ -	A	o	
	F	0.028	n.s
	M	o	
	Ne	0.155	n.s
♀ +	W	o	
	Ns	o	
	Ne	0.080	n.s
	WA	0.256	*
	R	0.202	n.s
	RW	0.153	**
	C	0.108	n.s

n.s : $p > 0.05$
* : $0.05 > p > 0.01$
** : $0.01 > p > 0.001$
*** : $0.001 > p$

o : Data too small for statistical comparison.

APPENDIX 3 f

Frequency distributions of time intervals between consecutive acts.

Statistical Comparison of ♂ and ♀ transitions.

KOLMOGOROV-SMIRNOV TEST

♂ to ♂ Transition	♂ to ♀ transitions with which ♂ to ♂ transition is compared			
	♂ to ♀-ve		♂ to ♀+ve	
	1971	1972	1971	1972
W → W	o	o	o	o
W → N	0.244 ***	0.231 **	0.284 ***	0.258 *
W → WA	o	o	o	o
Ns → Ne	0.293 ***	0.188 n.s	0.311 ***	0.258 *
N → WA	0.420 ***	0.119 n.s	0.186 n.s	0.165 n.s
N → RW	0.249 n.s	o	0.449 ***	o
WA → W			0.508 ***	0.113 n.s
WA → WA			0.610 ***	0.586 ***
RW → N			o	o
RW → WA			o	o

Each cell shows the value of D.

n.s : $p > 0.05$
* : $0.05 > p > 0.01$
** : $0.01 > p > 0.001$
*** : $0.001 > p$

o : Data too small for statistical comparison

APPENDIX 3 g

Derivation of H (see page 2/56).

If behaviour X leads to n other behaviours with frequencies of f_1, f_2, ... f_n, then the probability of occurrence of each transition is p_1, p_2, ... p_n, where $p = f \div N$ (N = total number of transitions from X).

The uncertainty value H of transitions from X is calculated by the formula:

$$H = \sum p_i \log_2 (1/p_i)$$

where i is successively all values from 1 to n.

H, measured in Bits, provides a measure of the predictability of transitions from X.

(Shannon and Weaver 1949, Dawkins and Dawkins in press.)

APPENDIX 3 h

Transition Intervals and Interruptions

TRANSITION	Total Frequency	Number Interrupted	% age Interrupted	Mean Transition Interval (secs)
M to W	477	1	0.2	0.4
W to OR	109	105	96.3	3.7
W to W	55	24	43.6	2.8
W to N	320	14	4.4	1.7
W to WA	60	15	25.0	3.0
W to RW	50	48	96.0	3.5
N to OR	151	119	78.8	3.2
N to WA	103	17	16.5	3.2
N to RW	90	32	35.6	1.3
WA to W	137	19	13.9	1.3
WA to WA	83	14	16.9	2.5
WA to RW	124	112	90.3	2.3
RW to N	74	34	45.9	2.1
RW to WA	98	53	54.1	3.4
RW to R	68	64	94.1	3.0
RW to RW	313	306	97.8	3.0
RW to C	110	101	91.8	2.3

1971 and 1972 data are combined.

APPENDIX 3 i

TRANSITIONS AFTER ♂ ACTIONS.

1st ♂ Act	♀ Int	2nd ♂ Act	1 sec intervals after 1st ♂ act						TOTAL
			1	2	3	4	5	5+	
W	-	OR	3	19	22	18	11	32	105
		W			3	1		2	6
		N			3	1	1	4	9
		WA				1		5	6
		RW							0
		O		2	5	6	3	8	24
		TOT	3	21	33	27	15	51	150
	0	OR		1		1	1	1	4
		W	8	7	5	8	2	1	31
		N	66	154	60	19	6	1	306
		WA	1	4	17	6	8	9	45
		RW				1		1	2
		O	10	4	6	3	1	18	42
		TOT	85	170	88	38	18	31	430
	+	OR							0
		W			5	2	1	10	18
		N			2	2		1	5
		WA			2		1	6	9
		RW		8	15	12	2	11	48
		O		5	5	6	4	7	27
		TOT	0	13	29	22	8	35	107
WA	-	OR		1	4	3	3	2	13
		W		1			1	2	4
		N							0
		WA				1	1	4	6
		RW				1			1
		O		1				2	3
		TOT	0	3	4	5	5	10	27
	0	OR	2	3	1			2	8
		W	51	33	21	9	2	2	118
		N	7	7	2	2		2	20
		WA	10	13	19	12	8	7	69
		RW	4	4		1		3	12
		O	4					7	11
		TOT	78	60	43	24	10	23	238
	+	OR							0
		W		4	5	3		3	15
		N		2	1				3
		WA			4	1	1	2	8
		RW	3	57	30	9	5	7	111
		O		3	5	3		4	15
		TOT	3	66	45	16	6	16	152

APPENDIX 3 i

(cont.)

TRANSITIONS AFTER ♂ ACTIONS

1st ♂ Act	♀ Int	2nd ♂ Act	1 sec intervals after 1st ♂ act						TOTAL
			1	2	3	4	5	5+	
RW	-	N							0
		WA					2	2	4
		R							0
		RW							0
		C							0
		O			2	2	2	6	12
		TOT	0	0	2	2	4	8	16
	0	N	3	14	15	7	1		40
		WA	2	6	10	10	2	15	45
		R	1	1	2				4
		RW	1	3	1	1	1		7
		C	1	4	2	1	1		9
		O		4	4	3	1		12
		TOT	8	32	34	22	6	15	117
	+	N		5	13	8	6	2	34
		WA		1	10	11	14	13	49
		R		8	21	22	10	3	64
		RW	1	68	110	66	34	27	306
		C	1	52	32	7	4	5	101
		O		3	5	1	3	2	14
		TOT	2	137	191	115	71	52	568
N	-	OR	7	24	18	19	9	41	118
		M	1	2	2	1	1		7
		W						1	1
		WA			1			3	4
		RW					1		1
		O		1	1	2		3	7
		TOT	8	27	22	22	11	48	138
	0	OR	9	12	4	5		3	33
		M	4	7	3	4	1	3	22
		W	3	5	2	1		7	18
		WA	2	24	14	10	4	32	86
		RW	21	29	6	1		1	58
		O	10	17		2	1	20	50
		TOT	49	94	29	23	6	66	267
	+	OR				1			1
		M							0
		W		1	4	4	3	8	20
		WA			1	2	1	9	13
		RW	1	6	7	3	3	11	31
		O		1	2	3	2	10	17
		TOT	1	8	14	13	9	38	83

APPENDIX 3 j

T. helveticus Fanning Bouts.

Frequency distributions of Bout Lengths.

UNINTERRUPTED BOUTS:

½ second intervals after start of Fanning Bouts.													
1	2	3	4	5	6	7	8	9	10	11	12	12+	TOT
3	24	11	7	7	13	5	2	3	5	6	4	81	170

INTERRUPTED BOUTS:

	17	5	3	2								1	28
	2	26	7	8	5	4	2			1		4	59
		2	10	6	6		1					1	26
			1	4	5	1	1	1				5	18

Each cell shows the number of Fan bouts that ended in a given half-second interval.

Only those interruptions that occurred in the first four half-second units are plotted.

APPENDIX 3 k

♀ Interruptions in ♂ to ♂ Transitions.

1971 Data:

♀ Interrupt	Successive ♂ to ♂ Transitions prior to first CREEP.																			
	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
+ ve		1	3	1	2	1	1	3	4	5	5	8	9	13	12	13	15	22	21	21
- ve	6	5	3	6	4	5	1	4	5	4	2	1	2	2	3	1	1			
0 (short)	7	8	9	8	10	8	14	9	6	9	14	11	8	6	8	8	6	1	2	2
0 (long)	2	2	2	2	1	4	2	3	3	1	3	4	2		1	1				
TOTAL	15	16	17	17	17	18	18	18	18	21	22	23	23	23	23	23	23	23	23	23

1972 Data:

+ ve			2		3	3	1	2	3	6	4	7	9	10	16	17	20	26	24	21
- ve	2	2	5	2	3	1	4	3	1	3	3	3		1	1		1			
0 (short)	9	8	7	12	9	13	11	12	9	12	12	10	9	11	10	9	6	2	4	7
0 (long)	2	4	2	3	3	2	3	4	6	2	4	4	9	6	1	2	2	1	1	1
TOTAL	13	14	16	17	18	19	19	19	19	23	23	24	27	28	28	28	29	29	29	29

0 (long) = those transitions with a transition interval longer than that time interval in which 75% of ♀ interruptions are observed to occur (see page 1/69).

APPENDIX 3 1

RESULTS OF ORIENTATION / DISPLAY EXPERIMENTS

Frequency of occurrence of ♂ acts during sustained periods of ♀ behaviour.

THE NEGATIVE / STATIC EXPT:

	F	M	W	N	WA	O	TOT
♀ MOVING AWAY	111	83	89	8		4	295
♀ STATIC		3	54	63	190	6	316

THE STATIC / POSITIVE EXPTS:

		W	N	WA	R	RW	O	TOT
♀ STATIC	Expt. 1	45	81	253			2	381
	Expt. 2	96	122	363			8	589
♀ APPROACHES	Expt. 1	4	36	9	65	169	6	289
	Expt. 2	1	24	2	51	148	2	228

ABBREVIATIONS: F: Follow; M: Move-to-the-Front; W: Whip; N: Fan; WA: Wave; R: Retreat; RW: Retreat-and-Whip; O: Others; TOT: Totals.

APPENDIX 3 m

TRANSITIONS AFTER QUIVER

Frequency distributions of time intervals between QUIVER and subsequent behaviours.

1 sec time intervals.	TOUCH TAIL		TURN BACK
	1971	Expt	Expt
1	18	21	
2	19	8	
3	11	2	
4	2	1	
5			
6	1		
7			1
8	1		1
9			1
10			1
11			3
12			1
13			2
14			2
15			2
16			2
17			3
18			1
19			1
20			1

1 sec time intervals	TOUCH TAIL		TURN BACK
	1971	Expt	Expt
21			
22			3
23			
24			1
25			
26			1
27			
28			1
29			2
30			
31			
32			
33			
34			
35			
36			
37			
38			1
39			
40			
TOTALS:	52	32	31

APPENDIX 4 a

DURATION OF FANNING BOUTS.

Bout Length 1 sec. Intervals.	T. vulgaris 1971	T. helveticus 1971	T. alpestris 1971
1	17	27	75
2	32	17	168
3	16	20	111
4	10	7	46
5	5	7	15
6	6	11	27
7	4	4	20
8	2	9	11
9	3	6	9
10	1	5	8
11		5	8
12	1	2	5
13	1	4	4
14	2	1	5
15	2	1	
16		4	1
17	2	2	5
18	3	1	5
19		6	3
20		1	1
20 +	3	29	13
TOTALS	110	169	540

Statistical Comparisons of Species.
KOLMOGOROV - SMIRNOV TEST:

T. vulgaris : T. helveticus;	D = 0.268	$p < 0.001$
T. vulgaris : T. alpestris;	D = 0.065	$p > 0.05$
T. alpestris : T. helveticus;	D = 0.321	$p < 0.001$

APPENDIX 4 b

RELATIVE FREQUENCIES OF ♂ DISPLAY ACTS

	M	W	N	WA	R	RW	TOT
T. vulgaris (1971)	278	365	258	190	95	354	1540
T. vulgaris (1972)	246	320	230	227	95	347	1465
T. vulgaris TOTAL:	524	685	488	417	190	701	3005
T. helveticus (1971)	107	247	558	191	46	206	1355

Statistical Comparisons

2 x 6 CHI^2 TEST:

T. vulgaris (1971) : *T. vulgaris* (1972) -

CHI^2 for 5 d.f = 8.0029. $p > 0.1$

T. vulgaris TOTAL : *T. helveticus* (1971) -

CHI^2 for 5 d.f = 354.46. $p < 0.001$

APPENDIX 4 c

ENCOUNTER AND SEQUENCE SUCCESS

	Sequences / Encounter		
	1	2	3
TOTAL ENCOUNTERS	9	16	20
SUCCESSFUL ENCOUNTERS	1	11	16

	SEQS./ ENC.	SEQUENCES		
		1st	2nd	3rd
TOTAL SEQUENCES	1	9		
	2	16	16	
	3	21	22	21
	TOT	45	38	21
SUCCESSFUL SEQUENCES	1	1		
	2	6	9	
	3	6	10	13
	TOT	13	19	13
MEAN POST-DEPOSITION TIME (secs)		17.0	29.8	32.8
MEAN NUMBER OF PUSH BACKS		0.5	2.0	2.5

APPENDIX 4 d

URODELE CLASSIFICATION

Order: URODELA (CAUDATA)

Sub order: CRYPTOBRANCHOIDEA

Family Hynobiidae
Family Cryptobranchidae

Sub order: SIRENOIDEA

Family Sirenidae

Sub order: SALAMANDROIDEA

Family Salamandridae
Family Proteidae
Family Amphiumidae

Sub order: AMBYSTOMATOIDEA

Family Ambystomatidae
Family Plethodontidae

(After Brame 1968)