

THE UNIVERSITY OF MANITOBA

A QUANTITATIVE NICHE COMPARISON OF THE WESTERN PLAINS
GARTER SNAKE (THAMNOPHIS RADIX HAYDENI) AND THE RED-SIDED
GARTER SNAKE (THAMNOPHIS SIRTALIS PARIETALIS) IN ALLOPATRIC
AND SYMPATRIC REGIONS OF MANITOBA'S INTERLAKE DISTRICT

BY

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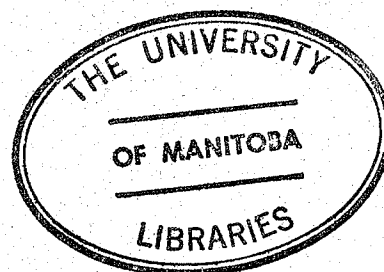
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MASTER OF SCIENCE

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ABSTRACT

THE NICHE OCCUPIED BY THE WESTERN PLAINS GARTER SNAKE (THAMNOPHIS RADIX HAYDENI) AND THE RED-SIDED GARTER SNAKE (THAMNOPHIS SIRTALIS PARIETALIS) IN THE INTERLAKE DISTRICT OF MANITOBA WERE COMPARED WITH RESPECT TO FEEDING HABITS AND SIX ENVIRONMENTAL FACTORS.

THAMNOPHIS SIRTALIS OCCURRING IN SYMPATRY WITH T. RADIX ALTERED ITS FEEDING HABITS, BUT NOT IN SUCH A WAY AS TO PRODUCE NICHE DISPLACEMENT. ITS FEEDING HABITS DID NOT DIFFER SIGNIFICANTLY FROM THOSE OF T. RADIX EITHER IN ALLOPATRY OR IN SYMPATRY. CHANGES IN ITS FEEDING HABITS ARE ATTRIBUTED TO CHANGES IN THE RELATIVE AVAILABILITY OF FOOD ITEMS.

OF THE ENVIRONMENTAL FACTORS EXAMINED, HABITAT, AIR TEMPERATURE AND SUBSTRATE TEMPERATURE CONTRIBUTED MOST STRONGLY TO NICHE DISCRIMINATION IN ALLOPATRY, T. RADIX OCCURRING NEAR MEADOW PONDS AT HIGH AIR BUT LOW SUBSTRATE TEMPERATURES AND T. SIRTALIS OCCURRING NEAR FEN-LIKE MARSHES OF THE ASPEN FOREST AT LOWER AIR BUT HIGHER SUBSTRATE TEMPERATURES. THAMNOPHIS SIRTALIS WAS ADAPTED TO LOWER AIR TEMPERATURES THAN T. RADIX BY VIRTUE OF ITS GREATER ABILITY TO ABSORB RADIANT ENERGY. IN SYMPATRY THE CONTRIBUTIONS OF HABITAT AND AIR TEMPERATURE TO NICHE DISCRIMINATION WERE REDUCED WHEREAS THOSE OF LIGHT INTENSITY AND SUBSTRATE TEMPERATURE WERE INCREASED, T. RADIX SELECTING A HIGHER VALUE OF BOTH THAN T. SIRTALIS. THIS SHIFT IN THE IMPORTANCE OF ENVIRONMENTAL FACTORS TO NICHE DISCRIMINATION NEED NOT BE ATTRIBUTED TO SPECIES INTERACTION BUT MAY BE EXPLAINED IN

TERMS OF BEHAVIORAL COMPENSATION FOR CONCURRENT CHANGES IN THE AVAILABLE NICHE. THE SHIFT WAS PRODUCED, IN PART, BY CHANGES IN THE DAILY ACTIVITY PATTERN, TOWARDS MID-DAY FOR T. RADIX AND AWAY FROM MID-DAY FOR T. SIRTALIS. THE DEGREE OF BIMODALITY IN THE ACTIVITY PATTERN WAS DIRECTLY PROPORTIONAL TO TEMPERATURE, AVAILABLE TEMPERATURES BEING LOWER IN SYMPATRY FOR T. RADIX AND HIGHER IN SYMPATRY FOR T. SIRTALIS.

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INTRODUCTION

THE SUMMER NICHE REQUIREMENTS OF GARTER SNAKES ARE POORLY KNOWN AND THE DEGREE OF COMPETITIVE INTERACTION BETWEEN SPECIES IS NOT KNOWN AT ALL. FOOD AND HABITAT UTILIZATION (CARPENTER, 1952; FLEHARTY, 1967) AND FOOD UTILIZATION (FOUQUETTE, 1954) HAVE BEEN COMPARED FOR SYMPATRIC POPULATIONS OF GARTER SNAKE SPECIES IN THREE WIDELY SEPARATED LOCALITIES. NONE OF THESE AUTHORS, HOWEVER, OBTAINED DETAILED COMPARATIVE DATA FOR ALLOPATRIC POPULATIONS OF THE SAME SPECIES. NICHE DISPLACEMENT AMONG SYMPATRIC GARTER SNAKES, WHILE SUGGESTED BY THESE AUTHORS AS A POSSIBLE EXPLANATION FOR RESOURCE PARTITIONING, HAS SELDOM BEEN PROPERLY EXAMINED. A NOTABLE EXCEPTION IS THE WORK IN PROGRESS OF WHITE AND KLOB (1974) ON SYMPATRIC POPULATIONS OF TWO GARTER SNAKE SPECIES IN CALIFORNIA, ONE OF WHICH IS REPRESENTED BY A NEARBY ALLOPATRIC POPULATION.

IN THE INTERLAKE DISTRICT OF MANITOBA TWO GARTER SNAKE SPECIES OCCUR: THE WESTERN PLAINS GARTER SNAKE (THAMNOPHIS RADIX HAYDENI KENNICOT) AND THE RED-SIDED GARTER SNAKE (THAMNOPHIS SIRTALIS PARIETALIS SAY). WHILE THE RANGE OF OVERLAP BETWEEN THESE SPECIES IS LIMITED, BOTH OCCUR IN SUFFICIENTLY LARGE NUMBERS TO ALLOW THE COLLECTION OF ADEQUATE SAMPLES FROM WITHIN THIS RANGE. THE PURPOSE OF THE PRESENT STUDY WAS TO COMPARE THE NICHE OCCUPIED BY THESE TWO SPECIES, BOTH WITHIN THE RANGE OF OVERLAP AND BEYOND IT, TO DETERMINE WHETHER ANY CHANGES IN THE RELATIVE NICHE POSITIONS WERE OCCURRING THAT COULD BE ATTRIBUTED TO THE PRESENCE OR ABSENCE OF A

CONGENERIC SPECIES RATHER THAN TO CHANGES IN THE AVAILABLE NICHE.

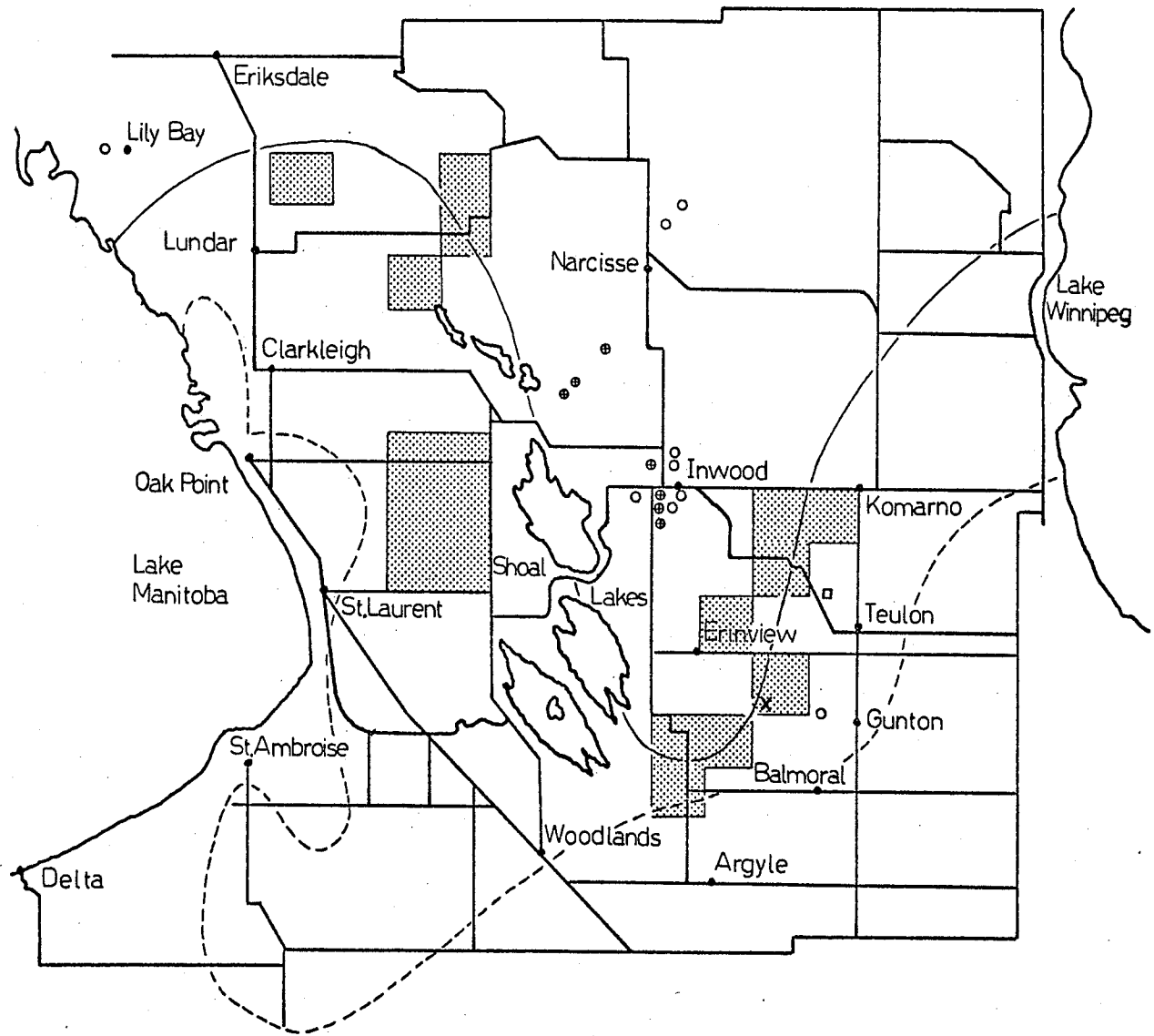
MATERIALS AND METHODS

FIELD STUDY

THE STUDY AREA IS LOCATED APPROXIMATELY BETWEEN 50° N AND 51° N LATITUDE AND BETWEEN 97° W AND 98° W LONGITUDE AND IS OUTLINED IN FIGURE 1. SNAKES WERE CAPTURED WITHIN THIS AREA FROM MAY THROUGH AUGUST OF 1973 AND FROM JUNE THROUGH AUGUST OF 1974. THE SAMPLING EFFORT IN 1974 WAS CONCENTRATED WITHIN A REGION DEFINED ON THE BASIS OF THE FIRST SUMMER'S SAMPLING AND INCLUDING ALL QUARTER-TOWNSHIPS (22.37 km²) IN WHICH BOTH I. RADIX AND I. SIRTALIS HAD BEEN CAPTURED. THIS REGION OF SYMPATRY IS SHOWN IN FIGURE 1. SEVERE FLOODING IN MAY OF 1974 PREVENTED SAMPLING IN THIS REGION BEFORE JUNE OF THAT SUMMER.

SNAKES WERE FOUND BY SEARCHING ON FOOT IN THE VICINITY OF WATER AND WERE CAPTURED BY HAND. ~~PRELIMINARY SAMPLING HAD SHOWN THAT SNAKES~~ WERE SELDOM FOUND FAR FROM A WATER BODY OF SOME SORT. SNAKES SEEN CROSSING ROADS WERE NOT CAPTURED SINCE THE ROAD HABITAT IS NOT A NATURAL ONE AND CANNOT BE AVOIDED BY SNAKES IN THEIR MOVEMENTS. THE SAMPLING EFFORT WAS SPREAD OVER THE DAYLIGHT HOURS FROM SUNRISE TO SUNSET SINCE PRELIMINARY ATTEMPTS TO FIND SNAKES AT NIGHT HAD PROVEN UNPRODUCTIVE. NO SYSTEMATIC SAMPLING PLAN WAS FOLLOWED DUE TO THE DIFFICULTY OF COLLECTING LARGE SAMPLES WITHOUT BEING SOMEWHAT OPPORTUNISTIC IN ALLOCATION OF THE SAMPLING EFFORT. ANY DEVELOPING BIAS IN COLLECTION WITH RESPECT TO TIME OF DAY, GEOGRAPHY OR WEATHER CONDITIONS WAS SOON DETECTED FROM FIELD RECORDS AND APPROPRIATE

FIGURE 1. MAP OF THE STUDY AREA. APPROXIMATE LINES OF CONTINUOUS (——) AND DISCONTINUOUS (-----) ASPEN FOREST ARE SHOWN. AREAS INCLUDED IN THE SYMPATRIC REGION ARE STIPLED. ALL OTHER AREAS ARE INCLUDED IN THE ALLOPATRIC REGION. THE KNOWN COMMUNAL DEN OF T. RADIX IS INDICATED BY AN OPEN SQUARE (□). KNOWN COMMUNAL DENS OF T. SIRTALIS ARE INDICATED BY OPEN CIRCLES (○). A CROSS IN THE DEN SYMBOL INDICATES FLOODING IN THE SPRING OF 1974. AN X INDICATES THE LOCATION OF TEMPERATURE STATIONS.



CORRECTIONS WERE MADE.

THE FEEDING HABITS OF T. RADIX AND T. SIRTALIS WERE EXAMINED BY PALPATING THE STOMACHS OF ALL SNAKES CAPTURED TO FORCE REGURGITATION OF RECENTLY EATEN FOOD. DUE TO THE DIFFICULTY OF DETERMINING THE NUMBER OF PREY REPRESENTED IN PARTIALLY DIGESTED REMAINS, ONLY THE PRESENCE, AND NOT THE NUMBER, OF FOOD ITEMS OF EACH TYPE FOUND IN A SNAKE WAS RECORDED.

SIX ENVIRONMENTAL FACTORS WERE RECORDED AT ALL CAPTURE SITES TO DETERMINE THE RELATIVE IMPORTANCE OF EACH OF THESE FACTORS AS NICHE DIMENSIONS. A NICHE DIMENSION IS DEFINED HERE AS ANY FACTOR SERVING TO SEPARATE SPECIES ECOLOGICALLY (LEVINS, 1967) AND THE IMPORTANCE OF AN ENVIRONMENTAL FACTOR REFERS HERE TO ITS VALUE IN SEPARATING T. RADIX AND T. SIRTALIS ECOLOGICALLY. ANYTHING OF POTENTIAL IMPORTANCE IN THIS RESPECT IS CONSIDERED AN ENVIRONMENTAL FACTOR. THE TERM IS USED, THEREFORE, IN ITS BROADEST SENSE.

HABITAT WAS CLASSIFIED AS AN ENVIRONMENTAL FACTOR ACCORDING TO THE TYPE OF WATER BODY NEAREST THE CAPTURE SITE OF A SNAKE. THREE CLASSES WERE RECOGNIZED REFLECTING THE PROPORTION OF WATER SURFACE AREA COVERED BY A SEDGE MAT. A SEDGE MAT WAS COMPOSED OF MOSS AND OLD SEDGE DECAYING JUST BENEATH THE SURFACE OF THE WATER AND OVERLAIN BY THE PREVIOUS YEAR'S GROWTH OF SEDGE, FOLDED TO FORM A COMPACT HORIZONTAL NETWORK AT OR ABOVE THE SURFACE OF THE WATER. HABITAT CLASSES INCLUDED PONDS (NO SEDGE MAT; SHARP INTERFACE BETWEEN LAND AND WATER), OPEN MARSHES (SEDEGE MAT AT THE EDGES ONLY; OPEN WATER OR SPARSE EMERGENT VEGETATION DOMINANT) AND CLOSED MARSHES (DOMINATED BY SEDGE MAT; LITTLE OR NO OPEN WATER). THE TERMINOLOGY OF AQUATIC COMMUNITIES IN THE ASPEN FOREST AND PARKLAND HAS NOT BEEN

STANDARDIZED. PONDS IN THE STUDY AREA CONFORMED TO THE DEFINITION OF RADFORTH (1964). HEINSELMAN (1963) INCLUDES THE MARSH TYPES REFERRED TO HERE AS OPEN AND CLOSED IN HIS DEFINITION OF MARSH. CLOSED MARSHES IN THE STUDY AREA RESEMBLED FENS BUT WERE NEITHER SUFFICIENTLY PEATY NOR SUFFICIENTLY PATTERNED TO CONFORM WELL TO HEINSELMAN'S DEFINITION OF THAT TERM. HABITAT CLASSES WERE CODED IN THE ABOVE ORDER FROM 1 THROUGH 3. A TRANSITION FROM THE FIRST HABITAT CLASS TO THE LAST WAS APPARENT ON A SOUTH-WEST TO NORTH-EAST CLINE THROUGH THE STUDY AREA CORRESPONDING TO A TRANSITION FROM PARKLAND TO ASPEN FOREST.

AIR AND SUBSTRATE TEMPERATURES AT STATIONS LOCATED IN THE ECOTONE BETWEEN PARKLAND AND ASPEN FOREST (FIG. 1) WERE OCCASIONALLY MONITORED IN AN ATTEMPT TO CHARACTERIZE THE HABITAT CLASSES ON THE BASIS OF THE RANGE OF ENVIRONMENTAL TEMPERATURES WHICH THEY OFFERED TO THE SNAKES. FOUR SUCH STATIONS WERE SET UP WITHIN 400 METRES OF ONE ANOTHER. ONE OF THESE WAS LOCATED IN A POND AT A WATER DEPTH OF 20 CM WITH MERCURY THERMOMETER BULBS FASTENED 5 CM ABOVE AND BELOW WATER LEVEL. ANOTHER WAS LOCATED IN THE MEADOW ADJACENT TO THIS POND WITH MERCURY THERMOMETER BULBS FASTENED 5 CM ABOVE AND BELOW SUBSTRATE LEVEL. A THIRD STATION WAS LOCATED IN CLOSED MARSH AT A WATER DEPTH OF 20 CM WITH MERCURY THERMOMETER BULBS FASTENED 5 CM BELOW WATER LEVEL, 5 CM ABOVE WATER LEVEL (BETWEEN THE WATER AND THE HORIZONTAL NETWORK OF OLD SEDGE OVERLYING IT) AND 15 CM ABOVE WATER LEVEL (ABOVE THE HORIZONTAL NETWORK OF OLD SEDGE). A FOURTH STATION WAS LOCATED IN THE ASPEN FOREST ADJACENT TO THIS MARSH WITH MERCURY THERMOMETER BULBS FASTENED 5 CM BELOW AND ABOVE SUBSTRATE LEVEL. ON SELECTED DAYS TEMPERATURES WERE TAKEN HOURLY AT THESE STATIONS BETWEEN SUNRISE AND SUNSET.

SUBSTRATE MOISTURE WAS CLASSIFIED AS AN ENVIRONMENTAL FACTOR ON THE BASIS OF A SIMPLE TEST PERFORMED AT THE CAPTURE SITE OF A SNAKE. IF WATER COULD NOT BE FORCED THROUGH THE FINGERS BY PRESSING THE BACK OF THE HAND AGAINST THE SUBSTRATE WITH AS MUCH FORCE AS POSSIBLE, THE SUBSTRATE WAS TERMED DRY. IF WATER COULD JUST BE FORCED THROUGH THE FINGERS BY SIMILAR ACTION, THE SUBSTRATE WAS TERMED DAMP. IF THE CUP OF THE HAND COULD BE FILLED WITH WATER BY SIMILAR ACTION, THE SUBSTRATE WAS TERMED WATERLOGGED. TWO ADDITIONAL MOISTURE CLASSES INCLUDED STANDING WATER (WITH EMERGENT VEGETATION) AND OPEN WATER (WITH NO EMERGENT VEGETATION). MOISTURE CLASSES WERE CODED IN THE ABOVE ORDER FROM 1 THROUGH 5. THIS CRUDE METHOD OF QUANTIFYING SUBSTRATE MOISTURE SEEMED TO CORRELATE WELL WITH THE AMOUNT OF WATER AT THE SURFACE UPON WHICH THE SNAKE WAS FOUND, AND WAS CONSIDERED PREFERABLE TO MEASUREMENTS OF WATER CONTENT FROM SOIL SAMPLES SINCE THE LATTER REFLECTED MOISTURE BENEATH THE SURFACE, WHICH OFTEN DIFFERED MARKEDLY FROM THAT FOUND AT THE SURFACE.

LIGHT INTENSITY INCIDENT UPON THE SNAKE AT ITS CAPTURE SITE WAS MEASURED AS AN ENVIRONMENTAL FACTOR WITH A VIVITAR PHOTOGRAPHIC LIGHT METER (MODEL 43). THE METER WAS SENSITIVE ONLY TO VISIBLE LIGHT. INTENSITY WAS RECORDED IN UNITS OF ELECTROMAGNETIC VALUE (EV) WITH THE LIGHT METER POINTED DIRECTLY AT THE SUN.

AIR TEMPERATURE AT SUBSTRATE LEVEL WAS RECORDED AT ALL CAPTURE SITES WITH YELLOW SPRINGS INCORPORATED (YSI) THERMISTORS (MODELS 43TD AND 42SC) AND YSI PROBES (MODEL 402).

SUBSTRATE TEMPERATURE WAS RECORDED AT ALL CAPTURE SITES WITH THE SAME THERMISTORS. SINCE SUBSTRATE TEMPERATURE NEAR THE SURFACE WAS EXTREMELY SENSITIVE TO THE DEPTH OF THE THERMISTER PROBE, TEMPERATURES

WERE TAKEN AT A DEPTH OF 5 CM BELOW THE SURFACE. AT THIS DEPTH MEASUREMENT ERROR COULD BE KEPT MINIMAL.

TIME OF CAPTURE OF EACH SNAKE WAS ALSO RECORDED AS AN ENVIRONMENTAL FACTOR. IT WAS CODED AS AN ABSOLUTE DEVIATION (IN HOURS) FROM 14:00 HOURS (2 P. M. AND THE APPROXIMATE MID-POINT OF THE DAY) SO AS TO REFLECT THE DEGREE OF BIMODALITY IN THE ACTIVITY PATTERN OF THE SNAKES. NO DISTINCTION WAS MADE WITH THIS TIME SCALE BETWEEN MORNING AND EVENING, SO THAT THE SCALE WOULD CORRELATE ROUGHLY WITH DIEL VARIATIONS IN ENVIRONMENTAL TEMPERATURE AND LIGHT INTENSITY. SUCH A SCALE WAS DESIRABLE IN ORDER THAT THE DEGREE OF CORRELATION OF TIME OF CAPTURE WITH TEMPERATURE OR LIGHT INTENSITY AT CAPTURE SITES WOULD SERVE AS AN INDICATOR OF THE EXTENT TO WHICH SNAKES WERE MAKING USE OF DIEL VARIATIONS IN SELECTING ENVIRONMENTAL TEMPERATURES OR LIGHT INTENSITIES.

THE SIX ENVIRONMENTAL FACTORS DESCRIBED ABOVE WERE FELT TO BE OF POTENTIAL IMPORTANCE IN CHARACTERIZING AND DISTINGUISHING BETWEEN THE NICHEs OF I. RADIX AND I. SIRTALIS. FOR AN ENVIRONMENTAL FACTOR TO BE IMPORTANT IN THIS SENSE IT IS NECESSARY, THOUGH NOT SUFFICIENT, THAT THE SNAKES BE SENSITIVE TO IT. ONE WAY IN WHICH ALL OF THE ENVIRONMENTAL FACTORS MEASURED SEEMED POTENTIALLY CAPABLE OF AFFECTING A SNAKE WAS BY MEANS OF INFLUENCING ITS BODY TEMPERATURE. TO DETECT SUCH INFLUENCES BOTH ORAL AND CLOACAL BODY TEMPERATURES OF THE SNAKES WERE TAKEN ALONG WITH MEASUREMENTS OF THE SIX ENVIRONMENTAL FACTORS AT EACH CAPTURE SITE. THE SAME THERMISTORS USED TO RECORD AIR AND SUBSTRATE TEMPERATURES WERE USED FOR THIS PURPOSE. BODY TEMPERATURES WERE ALWAYS TAKEN IMMEDIATELY UPON CAPTURE AND WITH MINIMAL HANDLING OF THE ANIMALS. THE TWO BODY TEMPERATURES WERE TAKEN CONSECUTIVELY AND

IN NO PARTICULAR ORDER.

FINALLY, AN ATTEMPT WAS MADE TO COMPARE MOVEMENTS OF I. RADIX AND I. SIRTALIS BY MARKING ALL INDIVIDUALS BEFORE RELEASE WITH A UNIQUE COMBINATION OF CLIPPED SUB-CAUDAL SCUTES (BLANCHARD AND FINSTER, 1933). INDIVIDUALS WERE FURTHER IDENTIFIED FOR FUTURE RECOGNITION BY SEX AND SNOUT-VENT MEASUREMENT.

DATA OF THE TYPE DESCRIBED ABOVE WERE TAKEN FROM 137 I. RADIX AND 128 I. SIRTALIS CAPTURED IN THE SUMMER OF 1973. OF THESE 32 I. RADIX AND 36 I. SIRTALIS WERE CAPTURED WITHIN THE SYMPATRIC REGION. AN ADDITIONAL SAMPLE OF 73 I. RADIX AND 32 I. SIRTALIS WAS COLLECTED FROM WITHIN THE SYMPATRIC REGION IN THE SUMMER OF 1974. DATA FROM THIS SAMPLE WERE POOLED WITH THOSE TAKEN FROM THE SAME REGION THE YEAR BEFORE.

LABORATORY STUDY

BODY TEMPERATURES OF SNAKES CAPTURED IN THE FIELD WERE RECORDED TO DETERMINE THEIR DEPENDENCY UPON ENVIRONMENTAL FACTORS AT THE CAPTURE SITE. SINCE SNAKES REQUIRE TIME TO COME TO THERMAL EQUILIBRIUM WITH THEIR ENVIRONMENT AND SINCE THE AMOUNT OF TIME SPENT BY SNAKES AT THEIR CAPTURE SITE PRIOR TO CAPTURE WAS IN MOST CASES UNKNOWN, THE RELATIONSHIPS BETWEEN BODY TEMPERATURE AND ENVIRONMENTAL FACTORS, AS DETERMINED FROM FIELD DATA, WERE EXPECTED TO SHOW A GREAT DEAL OF RESIDUAL VARIABILITY. THIS WAS EXPECTED TO BE ESPECIALLY TRUE OF THE RELATIONSHIP BETWEEN BODY TEMPERATURE AND LIGHT INTENSITY SINCE INCIDENT RADIATION COULD FLUCTUATE RAPIDLY WITH PASSING CLOUDS. RESIDUAL VARIABILITY WAS EXPECTED TO OBSCURE ANY DIFFERENCES IN THIS RELATIONSHIP WHICH MIGHT EXIST BETWEEN I. RADIX AND I. SIRTALIS. THEREFORE,

THE RATES AT WHICH I. RADIX AND I. SIRTALIS ABSORB RADIANT ENERGY WERE COMPARED DIRECTLY IN THE LABORATORY.

SNAKES WERE HELD IN A CIRCULAR STYROFOAM HEATING CHAMBER, 15.24 CM IN DIAMETER AND 2.54 CM IN DEPTH, WITH A TRANSPARENT ACETATE LID. A TUNGSTEN BULB WAS SUSPENDED OVER THIS CHAMBER AS A LIGHT SOURCE, PRODUCING AN INTENSITY OF 3875 LUX AT THE LEVEL OF THE CHAMBER LID. ALTHOUGH THE ACETATE LID TRANSMITTED SELECTIVELY IN THE VISIBLE REGION OF THE SPECTRUM, MUCH OF THE INFRA-RED RADIATION PRODUCED BY THE LIGHT SOURCE WAS ALLOWED TO REACH THE SNAKE AND ITS SUBSTRATE. SINCE STYROFOAM REFLECTS WELL AND CONDUCTS HEAT POORLY, SNAKES WERE ASSUMED TO DERIVE LITTLE BODY HEAT BY CONDUCTION FROM THE SUBSTRATE. THERMOMETER PROBES INSERTED ORALLY INTO THE SNAKE WERE HELD IN PLACE AT HEART LEVEL WITH MASKING TAPE OVER THE SNOUT. AIR TEMPERATURE WAS HELD AT 10° C.

SNAKES WERE TRANSFERRED TO THE HEATING CHAMBER AT A BODY TEMPERATURE OF 10° C, EQUAL TO THAT OF THE AIR. BODY TEMPERATURES ROSE AT A DECREASING RATE AND FINALLY STABILIZED. THE BODY TEMPERATURE AT WHICH EACH SNAKE STABILIZED FOR A PERIOD OF AT LEAST 15 MINUTES WAS DEFINED AS ITS EQUILIBRIUM TEMPERATURE. THE DIFFERENCE BETWEEN THIS TEMPERATURE AND THE INITIAL TEMPERATURE OF 10° C WAS DIVIDED BY THE TIME (IN MINUTES $\times 10^{-2}$) TAKEN TO ACHIEVE EQUILIBRIUM TO CALCULATE CRUDE WARMING RATES.

MUCH OF THE VARIABILITY IN THESE WARMING RATES WAS EXPECTED TO BE DUE TO VARIATION IN THE SIZE AND HENCE THE SURFACE AREA TO VOLUME RATIO OF THE SNAKES USED. THE SURFACE AREA TO VOLUME RATIO WAS ASSUMED TO APPROXIMATE AN INVERSE LINEAR FUNCTION OF TOTAL BODY LENGTH AND THE LATTER WAS RECORDED FOR EACH SNAKE AS A COVARIATE SO THAT VARIATION IN THE WARMING RATES DUE TO SIZE COULD BE ACCOUNTED FOR AND DIFFERENCES

IN THESE RATES BETWEEN I. RADIX AND I. SIRTALIS DETECTED MORE EASILY.

IT WAS FELT THAT SPECIES DIFFERENCES IN RATES OF ABSORBING RADIANT ENERGY MIGHT BE ATTRIBUTED TO DIFFERENCES IN COLOUR BETWEEN I. RADIX AND I. SIRTALIS. TO TEST THIS HYPOTHESIS, THE VISUAL ALBEDO OF EACH SNAKE WAS RECORDED, ALONG WITH TOTAL LENGTH, AS A COVARIATE SO THAT IT COULD BE DETERMINED WHETHER OR NOT ANY DIFFERENCES BETWEEN THE WARMING RATES OF I. RADIX AND I. SIRTALIS REMAINED AFTER VARIATION IN THESE RATES DUE TO VISUAL ALBEDO HAD BEEN ACCOUNTED FOR. VISUAL ALBEDO WAS MEASURED BY DIRECTING A COLLIMATED BEAM OF LIGHT AT THE SNAKE'S DORSAL SURFACE AND THEN RECORDING ITS REFLECTANCE WITH THE PHOTOGRAPHIC LIGHT METER. AN OPAQUE, FLAT-FINISHED, BLACK CARDBOARD TUBE, 5 CM IN LENGTH, WAS PLACED OVER THE APERTURE OF THE LIGHT METER TO EXCLUDE EXTRANEOUS LIGHT. SINCE THE LIGHT METER USED WAS INSENSITIVE TO INFRA-RED RADIATION, ALBEDO WAS MEASURED OVER A NARROWER RANGE OF THE SPECTRUM THAN THAT FROM WHICH THE WARMING SNAKES WERE RECEIVING RADIANT ENERGY.

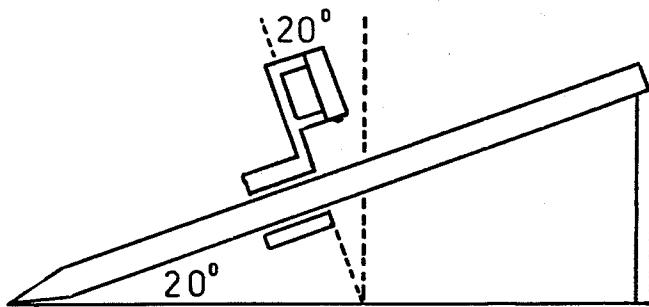
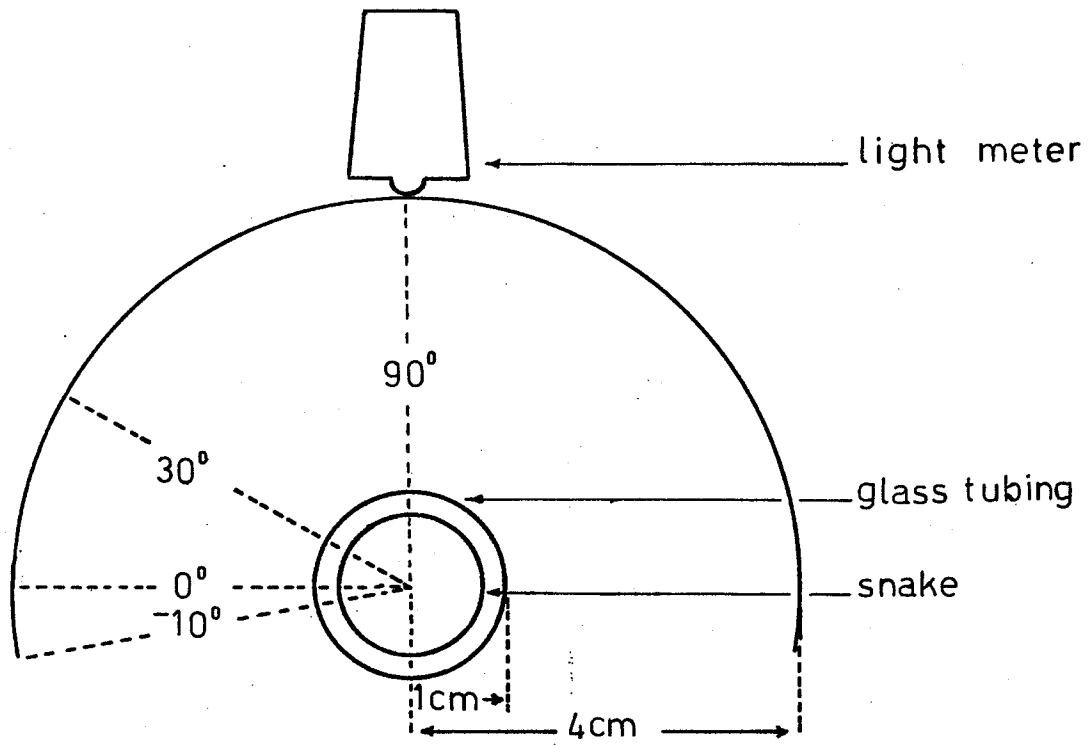
WARMING RATES OF DEAD SNAKES AND OF LIVING SNAKES WERE MEASURED. THE DEAD SNAKES SERVED AS A CONTROL TO SHOW THE EXTENT, IF ANY, TO WHICH PHYSIOLOGICAL AND BEHAVIORAL PROCESSES AFFECTED THE RATE OF HEAT GAIN IN LIVING SNAKES. TWENTY LIVING AND 20 DEAD SNAKES OF EACH SPECIES WERE USED.

TO DETERMINE WHERE ON THE BODY CIRCUMFERENCE THE GREATEST DIFFERENCES IN VISUAL ALBEDO OCCURRED, POINT REFLECTANCE OF DIFFUSE OVERHEAD LIGHT (969 LUX) WAS MEASURED BY HOLDING LIVING SNAKES OF BOTH SPECIES IN GLASS TUBING OF 2 CM DIAMETER, INCLINED AT 20° FROM THE HORIZONTAL. THE PHOTOGRAPHIC LIGHT METER WAS MOUNTED ON THE GLASS TUBING AND ROTATED IN 10° INTERVALS AROUND THE BODY CIRCUMFERENCE AT THE HEART LEVEL OF THE SNAKE IN A PLANE PERPENDICULAR TO THE LONG

AXIS OF THE TUBE WITH A RADIUS OF 4 CM FROM THE TUBE AXIS TO THE METER APERTURE (FIG. 2). THE CHOICE OF HEART LEVEL CIRCUMFERENCE WAS ARBITRARY SINCE, SUBJECTIVELY, COLOURATION WAS FAIRLY UNIFORM OVER THE LENGTH OF THE BODY BETWEEN THE BASE OF THE SKULL AND THE VENT. AS THE LIGHT METER WAS ROTATED TOWARDS THE DORSAL SURFACE OF THE GLASS TUBING, THE REFLECTANCE DETECTED BY THE LIGHT METER DECREASED DUE TO A SHADOWING EFFECT PRODUCED BY THE BODY OF THE LIGHT METER. AS THE MAGNITUDE OF THE REFLECTANCE DECREASED, THE MAGNITUDE OF DIFFERENCES IN REFLECTANCE BETWEEN I. RADIX AND I. SIRTALIS WAS CORRESPONDINGLY DECREASED. THE LIGHT METER PARTIALLY COMPENSATED FOR THIS EFFECT BY RECORDING REFLECTANCE IN THE LOGARITHMIC EV SCALE SO THAT DIFFERENCES IN REFLECTANCE WERE AMPLIFIED WHEN THE MAGNITUDE OF REFLECTANCE WAS LOW. THIS SCALE WAS RETAINED IN PRESENTATION OF THE RESULTS SO THAT SPECIES DIFFERENCES IN ALBEDO OVER THE DORSAL SURFACE OF THE SNAKE COULD BE SEEN MORE CLEARLY. THIRTY I. RADIX AND 27 I. SIRTALIS WERE EXAMINED BY THIS METHOD.

THE TIME OF CAPTURE OF SNAKES ENCOUNTERED IN THE FIELD WAS CODED SO AS TO CORRELATE ROUGHLY WITH DIEL VARIATIONS IN ENVIRONMENTAL TEMPERATURE AND LIGHT INTENSITY AND SO AS TO SERVE AS AN INDICATOR OF THE EXTENT TO WHICH SNAKES WERE MAKING USE OF THESE DIEL VARIATIONS IN SELECTING ENVIRONMENTAL TEMPERATURE AND LIGHT INTENSITY AT CAPTURE SITES. TO MAKE USE OF DIEL VARIATIONS IN THIS WAY, SNAKES MUST BE ABLE TO REGULATE THEIR DAILY ACTIVITY PATTERN SO AS TO BECOME MOST ACTIVE AT THE POINTS ON THE DIEL CYCLE WHEN ENVIRONMENTAL TEMPERATURES AND LIGHT INTENSITIES ARE OPTIMAL. TO DETERMINE WHETHER BOTH I. RADIX AND I. SIRTALIS WERE ABLE TO DO THIS THEIR PROFILES OF DAILY ACTIVITY WERE RECORDED AND COMPARED IN THE LABORATORY UNDER CONTROLLED TEMPERATURE

FIGURE 2. APPARATUS USED TO MEASURE ALBEDO AT SELECTED POINTS
AROUND THE BODY CIRCUMFERENCE OF T. RADIX AND T. SIRTALIS. A
CROSS SECTION (ABOVE) AND A LATERAL VIEW (BELOW) ARE SHOWN.



AND LIGHT REGIMES.

A NIGHT TEMPERATURE OF 10° C WAS USED WITH DAY TEMPERATURES OF 20° C, 32° C AND 40° C. LIGHT INTENSITY VARIED IN FIVE EQUAL STEPS BETWEEN 7:00 A. M. AND 9:00 P. M. PEAKING AT 1722 LUX BETWEEN 12:00 NOON AND 4:00 P. M. SNAKES WERE ENCLOSED IN A TERRARIUM WHICH COVERED 3.34 M² WITH 0.28 M² OF SHADE IN EACH CORNER, WITH SAND AND SAWDUST SUBSTRATE ON THE FLOOR, AND A SHALLOW PAN OF WATER 0.09 M² IN A MOUND OF SUBSTRATE IN THE CENTRE. BOARDS, UNDER WHICH THE SNAKES COULD HIDE, WERE PLACED IN THE SHADE AND IN THE OPEN TO PROVIDE COMPLETE COVER FROM THE LIGHT.

TEN I. RADIX (5 MALES AND 5 FEMALES) AND 10 I. SIRTALIS (5 MALES AND 5 FEMALES) WERE ENCLOSED TOGETHER IN THE TERRARIUM AT THE BEGINNING OF EACH EXPERIMENT. ONE EXPERIMENT WAS RUN AT EACH OF THE THREE DAY-TIME TEMPERATURES. SNAKES WERE ACCLIMATED FOR A PERIOD OF THREE DAYS, OBSERVED FOR THREE DAYS AND THEN REPLACED BY NEW SNAKES WHICH WERE AGAIN ACCLIMATED FOR A PERIOD OF THREE DAYS AND THEN OBSERVED FOR THREE DAYS. DURING OBSERVATION PERIODS THE TOTAL NUMBER OF ACTIVE SNAKES OF EACH SPECIES WAS RECORDED HOURLY. ANY SNAKE EXPOSED TO VIEW RATHER THAN HIDDEN UNDER A BOARD WAS CONSIDERED TO BE ACTIVE. THE NUMBER OF THESE ACTIVE SNAKES EXPOSED IN THE OPEN AS OPPOSED TO SHADE, AND THE NUMBER OF THOSE EXPOSED IN THE OPEN WHICH WERE IN THE WATER PAN WERE ALSO RECORDED FOR EACH SPECIES. A TOTAL OF SIX DAYS' OBSERVATIONS WAS COLLECTED AT EACH DAY TEMPERATURE.

ANALYTICAL METHODS

FEEDING HABITS OF I. RADIX AND I. SIRTALIS WERE COMPARED, BOTH IN ALLOPATRIC AND IN SYMPATRIC REGIONS, USING A CHI-SQUARE TEST FOR ASSOCIA-

TION BETWEEN SPECIES AND FOOD TYPE UTILIZED. FEEDING HABITS IN ALLOPATRIC AND SYMPATRIC REGIONS WERE ALSO COMPARED, BOTH FOR I. RADIX AND I. SIRTALIS, USING A CHI-SQUARE TEST FOR ASSOCIATION BETWEEN REGION AND FOOD TYPE UTILIZED.



SAMPLING EFFORT IN THE FIELD WAS ESTIMATED FOR EACH SPECIES IN HOURS SPENT SEARCHING FOR SNAKES WITHIN ITS RANGE. DAILY PROFILES OF CATCH PER UNIT EFFORT, CALCULATED FOR HOURLY, INTERVALS THROUGHOUT THE COURSE OF THE DAY, WERE COMPARED BETWEEN I. RADIX AND I. SIRTALIS BOTH IN ALLOPATRIC AND IN SYMPATRIC REGIONS. FOR INTERVALS IN WHICH LESS THAN THREE SEARCH HOURS HAD BEEN SPENT CATCH PER UNIT EFFORT WAS NOT CALCULATED.

SLIGHT BIASES OFTEN DEVELOPED IN THE SAMPLING EFFORT BEFORE THEY WERE NOTICED AND CORRECTED. THE EFFORT SPENT SEARCHING FOR I. RADIX AND I. SIRTALIS VARIED SLIGHTLY THROUGHOUT THE SUMMER IN FAVOUR OF EITHER ONE SPECIES OR THE OTHER. SINCE THE RANGE OF ENVIRONMENTAL FACTORS AVAILABLE TO THE SNAKES ALSO VARIED THROUGHOUT THE COURSE OF THE SUMMER, SUCH DISPARATE SEASONAL ALLOCATION OF THE SAMPLING EFFORT WAS LIKELY TO PRODUCE SPURIOUS DIFFERENCES BETWEEN SPECIES IN THE RANGE OF ENVIRONMENTAL FACTORS MEASURED AT CAPTURE SITES. THEREFORE, SEASONAL TRENDS IN ENVIRONMENTAL FACTORS WERE QUANTIFIED SO THAT ENVIRONMENTAL DATA FROM CAPTURE SITES COULD BE ADJUSTED FOR THESE TRENDS BY COVARIANCE, USING POWERS OF THE DATE AS COVARIATES. THIS METHOD OF COMPENSATING FOR SEASONAL EFFECTS IN LONG TERM DATA WAS USED BY GREEN (1974) IN A SIMILAR TYPE OF STUDY. SECOND ORDER POLYNOMIALS OF CAPTURE DATE WERE USED TO DESCRIBE SEASONAL TRENDS IN THE ENVIRONMENTAL FACTORS AS PARABOLIC CURVES. ON THE BASIS OF VISUAL INSPECTION OF THE SCATTER OF POINTS ABOUT THESE CURVES, THIS DESCRIPTION WAS CONSIDERED TO BE ADEQUATE.

THE FREQUENCY DISTRIBUTIONS OF ENVIRONMENTAL FACTORS WERE OFTEN

NON-NORMAL. MEDIANS OFTEN DIFFERED SIGNIFICANTLY FROM THE MEANS INDICATING SKEWNESS AND 95% CONFIDENCE INTERVALS OFTEN EXCEEDED OR FELL SHORT OF THE MEASURED RANGE INDICATING KURTOSIS (FIG. 3). WITH LARGE SAMPLES NON-NORMALITY HAS LITTLE EFFECT UPON COMPARISONS OF THE MEANS EITHER BY UNIVARIATE (SCHEFFÉ, 1959) OR BY MULTIVARIATE (ITO IN KRISHNAIAH, 1969) METHODS, ALTHOUGH IT MAY INFLUENCE COMPARISONS OF VARIANCE AND COVARIANCE MORE STRONGLY. HETEROGENEITY OF VARIANCE, WHICH OFTEN ACCOMPANIES NON-NORMALITY, WAS CONSIDERED MORE OF A PROBLEM. ALTHOUGH UNIVARIATE COMPARISONS OF MEANS ARE LITTLE AFFECTED BY HETEROGENEITY OF VARIANCE WHEN SAMPLE SIZES ARE LARGE, MOST ASSERTIONS ABOUT ROBUSTNESS WITH RESPECT TO THE ASSUMPTION OF HOMOGENEITY OF VARIANCE IN THE MULTIVARIATE CASE ARE SPECULATIVE AND CARE SHOULD BE TAKEN TO MINIMIZE VIOLATION OF THIS ASSUMPTION (PRESS, 1972).

THE MEANS OF ENVIRONMENTAL FACTORS FOR I. RADIX AND I. SIRTALIS WERE COMPARED BOTH BY UNIVARIATE AND MULTIVARIATE METHODS. LARGE SAMPLE NORMAL DEVIATE TESTS WERE USED FOR UNIVARIATE COMPARISONS AND THESE WERE APPLIED TO ENVIRONMENTAL DATA THAT HAD NOT BEEN ADJUSTED FOR SEASONAL TRENDS. THE REASON FOR THIS WAS THAT SEASONAL TRENDS SHOWN BY TWO OF THE ENVIRONMENTAL FACTORS DIFFERED SIGNIFICANTLY BETWEEN SPECIES (FIG. 4). IN THESE CASES THE DESCRIPTION AND USE OF COMMON SEASONAL TRENDS TO ADJUST THE ENVIRONMENTAL DATA FOR LONG TERM EFFECTS WAS NOT STRICTLY JUSTIFIED. DISCRIMINANT FUNCTION ANALYSIS WAS USED FOR MULTIVARIATE COMPARISON OF ENVIRONMENTAL FACTORS BETWEEN I. RADIX AND I. SIRTALIS. THIS METHOD (COOLEY AND LOWNES, 1971) WAS APPLIED TO ENVIRONMENTAL DATA THAT HAD BEEN ADJUSTED FOR SEASONAL TRENDS. THE REASON FOR THIS WAS THAT SEASONAL ADJUSTMENT OF THE ENVIRONMENTAL DATA IMPROVED MULTIVARIATE HOMOGENEITY OF VARIANCE. ALTHOUGH THE USE OF

FIGURE 3. LOCATION OF I. RADIX () AND I. SIRTALIS () ON GRADIENTS OF THE SIX ENVIRONMENTAL FACTORS MEASURED AT CAPTURE SITES. RECTANGLES INDICATE 95% CONFIDENCE INTERVALS ON THE MEANS (•). MEDIANS (◦) AND 95% CONFIDENCE INTERVALS ON THE OBSERVATIONS (—) ARE ALSO SHOWN. THE AXIS OF AN ENVIRONMENTAL FACTOR IS BROKEN (---) BEYOND THE MEASURED RANGE OF THAT FACTOR. STATISTICS ABOVE THE AXIS PERTAIN TO THE ALLOPATRIC REGION. STATISTICS BELOW THE AXIS PERTAIN TO THE SYMPATRIC REGION.

TIME IS MEASURED IN UNITS OF HOURS \pm 2 P. M. QUALITATIVE FACTORS ARE CODED AS FOLLOWS:

| CODE | HABITAT | MOISTURE |
|------|--------------|----------------|
| 1 | POND | DRY |
| 2 | OPEN MARSH | DAMP |
| 3 | CLOSED MARSH | WATERLOGGED |
| 4 | | STANDING WATER |
| 5 | | OPEN WATER |

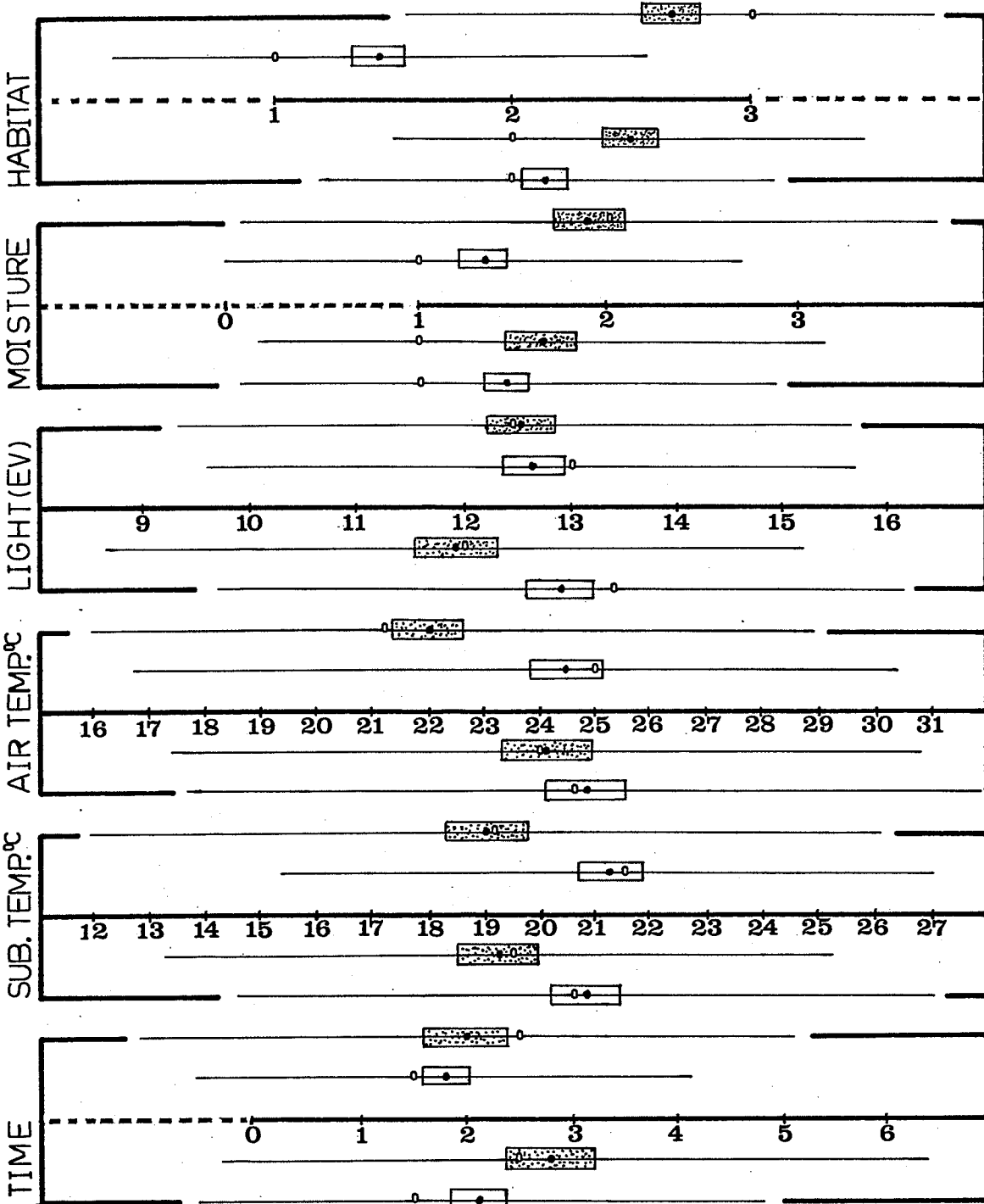
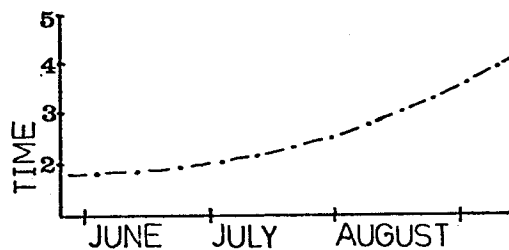
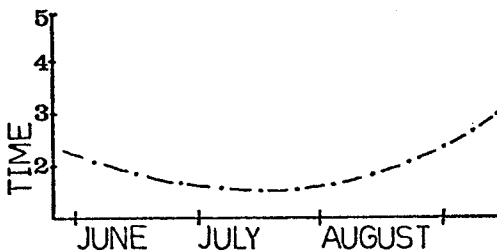
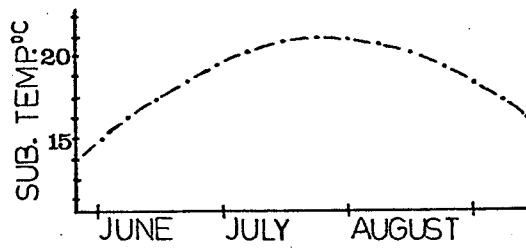
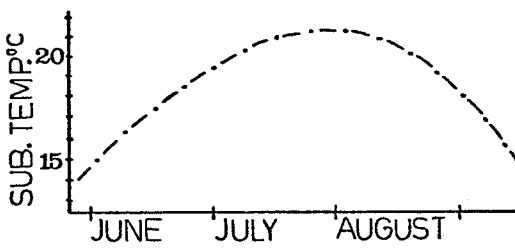
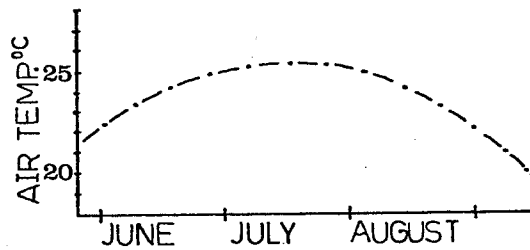
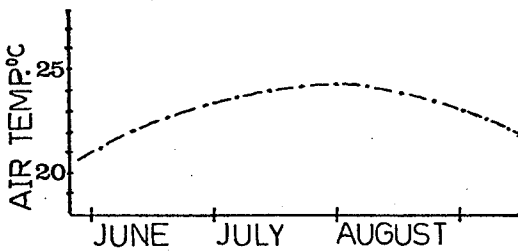
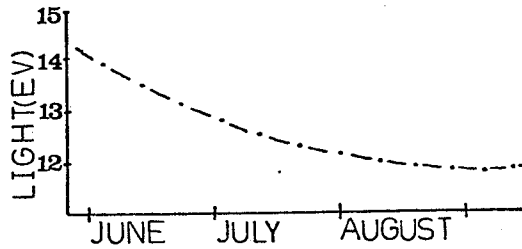
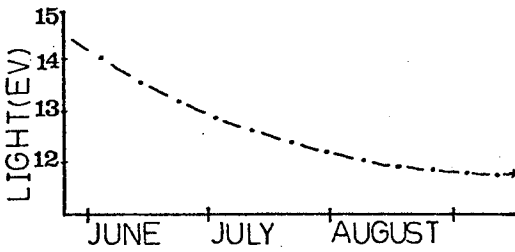
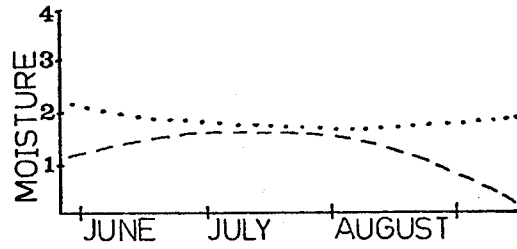
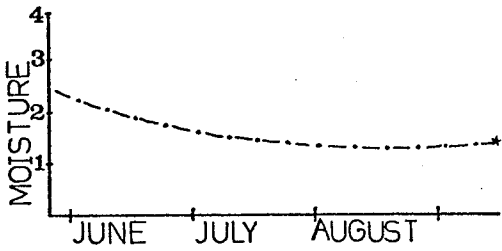
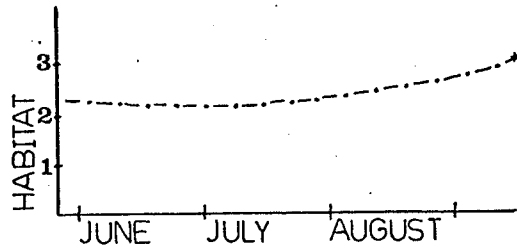
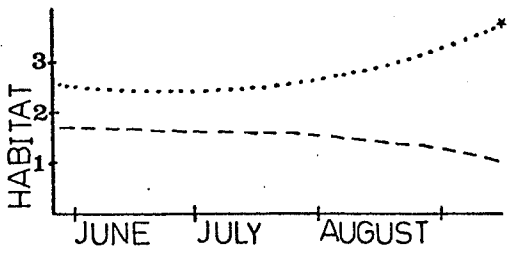


FIGURE 4. SEASONAL TRENDS IN THE ENVIRONMENTAL FACTORS MEASURED AT CAPTURE SITES. FACTOR UNITS AS IN FIGURE 3. TRENDS FOR T. RADIX (----) AND T. SIRTALIS (.....) ARE SHOWN SEPARATELY WHERE THEY DIFFER SIGNIFICANTLY ($P < .01$) AND ARE OTHERWISE POOLED (----). SIGNIFICANT TRENDS ($P < .01$) ARE INDICATED BY A STAR (*). TRENDS IN THE ALLOPATRIC REGION ARE SHOWN ON THE LEFT. TRENDS IN THE SYMPATRIC REGION ARE SHOWN ON THE RIGHT.



SEASONALLY ADJUSTED DATA MAY HAVE BEEN SOMEWHAT ARTIFICIAL SINCE NOT ALL ENVIRONMENTAL FACTORS SHOWED SEASONAL TRENDS THAT WERE COMMON TO BOTH SPECIES, UNCERTAINTY ABOUT THE ROBUSTNESS OF MULTIVARIATE METHODS TO VIOLATIONS OF THE HOMOGENEITY OF VARIANCE ASSUMPTION MADE THE USE OF SEASONALLY ADJUSTED ENVIRONMENTAL DATA PREFERABLE FOR MULTIVARIATE COMPARISON. MULTIVARIATE COMPARISON WAS CONSIDERED MORE INFORMATIVE THAN UNIVARIATE COMPARISON BECAUSE IT TAKES CORRELATIONS BETWEEN THE ENVIRONMENTAL FACTORS INTO CONSIDERATION.

THE METHOD OF DISCRIMINANT ANALYSIS AS USED HERE IS ANALOGOUS TO A MULTIPLE REGRESSION OF A DUMMY VARIABLE REFLECTING SPECIES MEMBERSHIP UPON A SET OF ENVIRONMENTAL FACTORS. ENVIRONMENTAL FACTORS WHICH CONTRIBUTE STRONGLY TO DISCRIMINATION BETWEEN THE NICHES OF T. RADIX AND T. SIRTALIS ARE WEIGHTED HEAVILY IN THE MULTIPLE REGRESSION EQUATION, OR DISCRIMINANT FUNCTION, SO AS TO MAXIMIZE THE RATIO OF BETWEEN SPECIES TO WITHIN SPECIES VARIABILITY IN THE PREDICTED VALUES OF THE DUMMY VARIABLE. THESE PREDICTED VALUES ARE CALLED DISCRIMINANT SCORES. EACH SNAKE WAS THEREFORE ASSIGNED A DISCRIMINANT SCORE WHICH WAS A LINEAR FUNCTION OF THE ENVIRONMENTAL FACTORS MEASURED AT ITS CAPTURE SITE. THE DIFFERENCE BETWEEN THE MEAN DISCRIMINANT SCORE OF T. RADIX AND T. SIRTALIS IS A MEASURE OF THE OVERALL ECOLOGICAL DISTANCE BETWEEN THEIR NICHES. AN INCREASE IN THIS DISTANCE WHEN SNAKES ARE COLLECTED FROM A REGION OF SYMPATRY CAN BE TAKEN AS EVIDENCE OF NICHE DISPLACEMENT. THE MAGNITUDE OF WEIGHTS ASSIGNED TO EACH ENVIRONMENTAL FACTOR IN THE DISCRIMINANT FUNCTION DEPENDS NOT ONLY UPON ITS IMPORTANCE TO SPECIES DISCRIMINATION BUT ALSO UPON THE MAGNITUDE OF THE UNITS OF MEASUREMENT FOR THAT FACTOR. STANDARDIZATION OF THE WEIGHTS EQUALIZES THE SCALE OF MEASUREMENT SO THAT THE STANDARDIZED WEIGHTS REPRESENT THE RELATIVE PROPORTION OF SPECIES DISCRIMINATION CONTRIBUTED TO THE FUNCTION BY EACH ENVIRONMENTAL FACTOR.

MULTIPLICATION OF STANDARDIZED WEIGHTS BY THE DISCRIMINATING POWER OF THE ENTIRE FUNCTION GIVES AN INDEX OF THE ECOLOGICAL IMPORTANCE OF EACH FACTOR WHICH CAN BE COMPARED BETWEEN DIFFERENT DISCRIMINANT FUNCTIONS. THE MEASURE OF DISCRIMINATING POWER USED HERE WAS THE SQUARED CANNONICAL CORRELATION COEFFICIENT BETWEEN THE DUMMY SPECIES VARIABLE AND THE ENVIRONMENTAL FACTORS, WHICH REPRESENTS THE FRACTION OF VARIATION IN SPECIES MEMBERSHIP EXPLAINED BY THE DISCRIMINANT FUNCTION. THE INDEX SO PRODUCED WAS USED TO COMPARE THE ECOLOGICAL IMPORTANCE OF ENVIRONMENTAL FACTORS BETWEEN ALLOPATRIC AND SYMPATRIC REGIONS. THE SIGN OF THIS INDEX FOR ANY ONE FACTOR INDICATED THE RELATIVE POSITION OF T. RADIX AND T. SIRTALIS ON THAT ENVIRONMENTAL GRADIENT, A NEGATIVE SIGN INDICATING THAT T. RADIX WAS LOCATED AT THE LOWER END OF THAT GRADIENT AND T. SIRTALIS AT THE UPPER END.

SINCE MULTIVARIATE METHODS TAKE CORRELATIONS BETWEEN FACTORS INTO CONSIDERATION, CORRELATION COEFFICIENTS AND NORMAL DEVIATE TESTS OF THEIR SIGNIFICANCE WERE CALCULATED BETWEEN ALL PAIRS OF ENVIRONMENTAL FACTORS IN ORDER TO EXPLAIN POSSIBLE DISCREPANCIES BETWEEN UNIVARIATE AND MULTIVARIATE RESULTS. CORRELATIONS WERE COMPUTED SEPARATELY FOR T. RADIX AND T. SIRTALIS.

TO DETERMINE THE DEGREE OF DEPENDENCE OF BODY TEMPERATURES UPON THE ENVIRONMENTAL FACTORS, MULTIPLE REGRESSIONS OF ORAL AND CLOACAL TEMPERATURES ON THESE FACTORS WERE CALCULATED SEPARATELY FOR T. RADIX AND T. SIRTALIS. NORMAL DEVIATE TESTS WERE USED TO COMPARE SLOPES AND INTERCEPTS BETWEEN SPECIES.

SINCE ONLY TWO FEMALE T. SIRTALIS WERE RECAPTURED, NO ANALYSIS OF MOVEMENTS WAS POSSIBLE.

STEPWISE FACTORIAL ANALYSIS OF COVARIANCE WAS USED TO COMPARE THE

WARMING RATES OF I. RADIX AND I. SIRTALIS IN THE LABORATORY, FIRST ELIMINATING VARIABILITY DUE TO TOTAL LENGTH AND THEN ELIMINATING VARIABILITY DUE TO VISUAL ALBEDO TO SEE IF ANY RATE DIFFERENCES REMAINED BETWEEN SPECIES. STATES (ALIVE OR DEAD) AND SPECIES WERE USED AS FACTORS. SINCE INTERACTION BETWEEN THESE FACTORS MADE INTERPRETATION OF THE RESULTS DIFFICULT, THE ANALYSIS WAS REPEATED USING DEAD SNAKES ONLY. THE WARMING RATES OF LIVING SNAKES HAD BEEN STRONGLY AFFECTED BY ESCAPE BEHAVIOR WHICH DIFFERED MARKEDLY BETWEEN SPECIES.

COMPARISON BETWEEN I. RADIX AND I. SIRTALIS OF VISUAL ALBEDO PATTERNS AROUND THE BODY CIRCUMFERENCE WAS MADE BY CALCULATING 95% CONFIDENCE INTERVALS FOR EACH SPECIES ON THE MEAN REFLECTANCE AT EACH POINT EXAMINED ON THE BODY CIRCUMFERENCE.

COMPARISON OF THE DAILY ACTIVITY PATTERNS OF I. RADIX AND I. SIRTALIS UNDER CONTROLLED TEMPERATURE AND LIGHT REGIMES WAS MADE BY CALCULATING 95% CONFIDENCE INTERVALS FOR EACH SPECIES ON THE MEAN OF THE HOURLY TOTALS FOR NUMBER OF SNAKES EXPOSED TO VIEW. BINOMIAL CONFIDENCE INTERVALS WERE USED SINCE THE EXPOSURE OF A SNAKE TO VIEW IS A BINOMIAL EVENT.

RESULTS

FEEDING HABITS

FROM TABLE 1 IT WAS APPARENT THAT THERE WERE NO DIFFERENCES IN THE FEEDING HABITS OF I. RADIX AND I. SIRTALIS EITHER IN THE ALLOPATRIC REGION ($\chi_7^2 = 9.66$; $P > .01$) OR IN THE SYMPATRIC REGION ($\chi_6^2 = 10.47$; $P > .01$). THE FEEDING HABITS OF I. RADIX DID NOT DIFFER BETWEEN ALLOPATRIC AND SYMPATRIC REGIONS ($\chi_8^2 = 11.68$; $P > .01$). THE FEEDING HABITS OF I. SIRTALIS DID DIFFER BETWEEN ALLOPATRIC AND SYMPATRIC REGIONS ($\chi_4^2 = 13.42$; $P < .01$). THE CHANGE INVOLVED AN INCREASED UTILIZATION IN THE SYMPATRIC REGION OF WOOD FROGS (RANA SYLVATICA) AND A DECREASED UTILIZATION OF CHORUS FROGS (PSEUDACRIS TRISERIATA).

ENVIRONMENTAL FACTORS

SEASONAL TRENDS IN THE ENVIRONMENTAL FACTORS WERE ADEQUATELY DESCRIBED AS PARABOLIC FUNCTIONS OF THE DATE (FIG. 4). HABITAT, AS RECORDED AT CAPTURE SITES, WAS AFFECTED BY SEASONAL MOVEMENTS OF THE SNAKES IN THE ALLOPATRIC REGION. AS I. SIRTALIS MOVED NORTH IN THE FALL TOWARDS ITS DENING SITES, IT WAS FOUND MORE FREQUENTLY NEAR THE CLOSED MARSHES OF THE ASPEN FOREST. A SLIGHT SHIFT IN I. RADIX TOWARDS THE PONDS OF THE OPEN PARKLAND TO THE SOUTH WAS NOT SIGNIFICANT, BUT THE TRENDS FOR I. RADIX AND I. SIRTALIS DIFFERED SIGNIFICANTLY FROM ONE ANOTHER IN THE ALLOPATRIC REGION. IN THE RESTRICTED SYMPATRIC REGION SEASONAL MOVEMENTS OF THE SNAKES HAD LESS EFFECT ON HABITAT CLASSES AND NO SIGNIFICANT SEASONAL TRENDS WERE SHOWN. MOISTURE, AS RECORDED AT

TABLE 1. FREQUENCY OF OCCURRENCE OF FOOD ITEMS IN STOMACHS OF
T. RADIX AND T. SIRTALIS IN ALLOPATRIC AND IN SYMPATRIC REGIONS

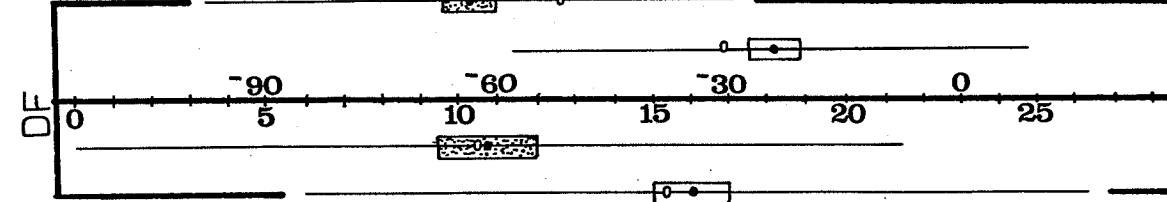
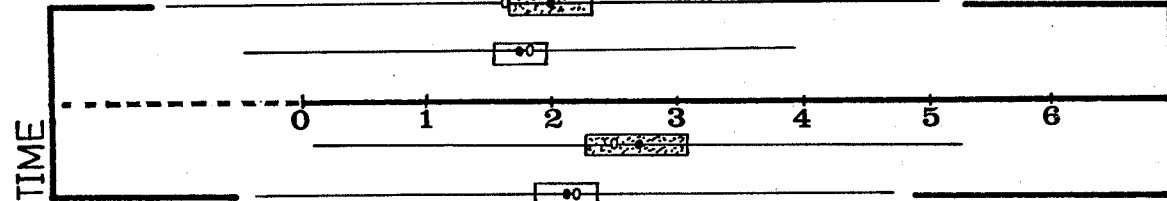
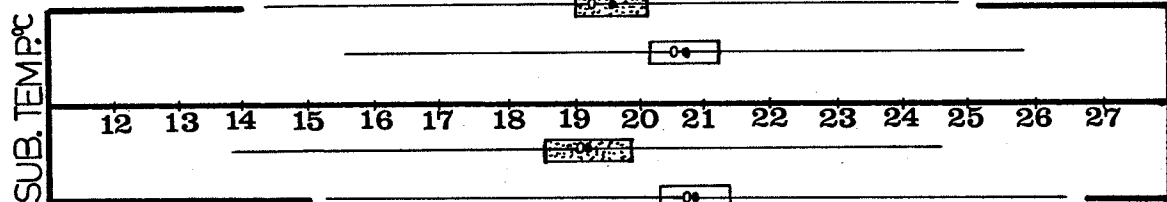
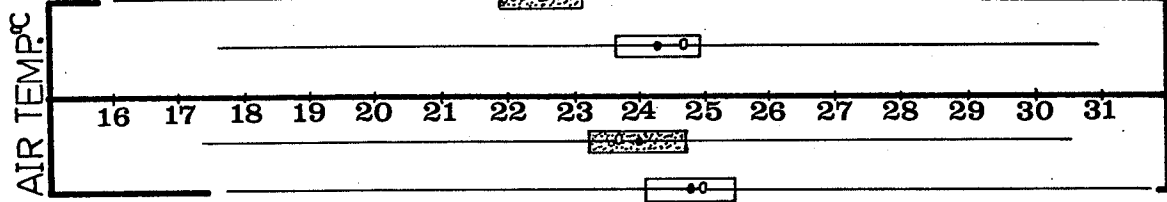
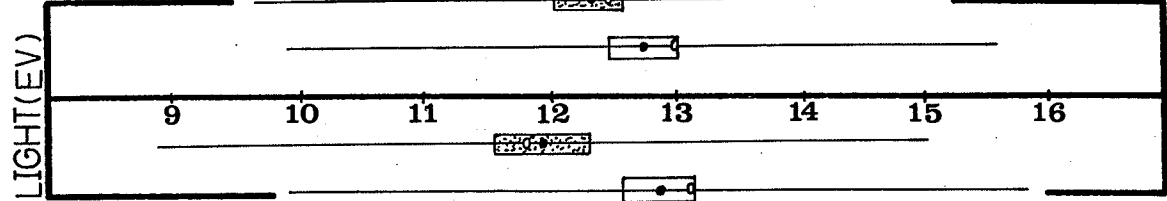
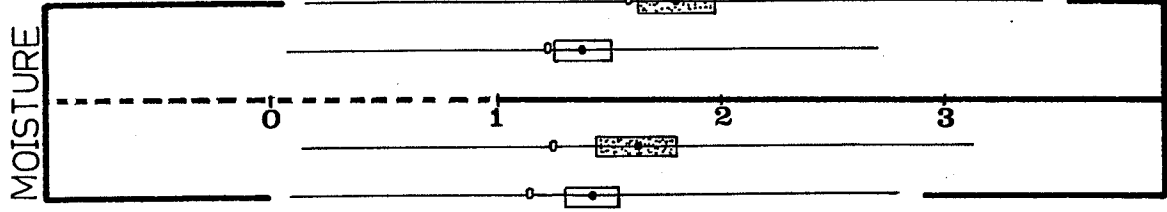
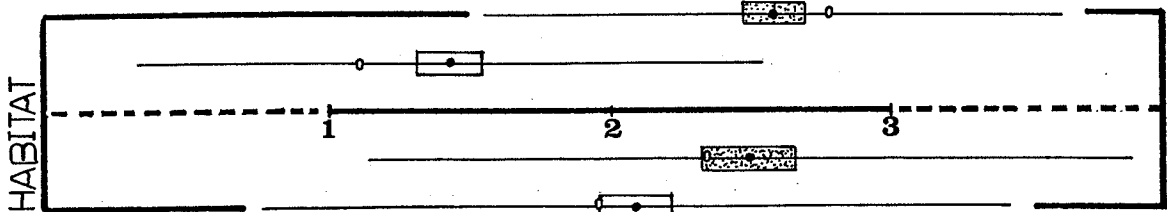
| FOOD CLASS | <u>ALLOPATRIC REGION</u> | | <u>SYMPATRIC REGION</u> | |
|------------------------------|--------------------------|--------------------|-------------------------|--------------------|
| | <u>T. RADIX</u> | <u>T. SIRTALIS</u> | <u>T. RADIX</u> | <u>T. SIRTALIS</u> |
| <u>RANA SYLVATICA</u> | 24 | 15 | 36 | 24 |
| <u>RANA PIPIENS</u> | 4 | 0 | 3 | 0 |
| <u>PSEUDACRIS TRISERIATA</u> | 8 | 11 | 7 | 4 |
| <u>HYLA VERSICOLOR</u> | 2 | 2 | 1 | 3 |
| <u>BUFO</u> | 3 | 3 | 4 | 2 |
| TADPOLES | 5 | 0 | 1 | 0 |
| RODENTIA | 1 | 0 | 1 | 0 |
| OLIGOCHAETA | 5 | 2 | 0 | 0 |
| HIRUDINA | 6 | 6 | 6 | 0 |
| GASTROPODA | 0 | 0 | 2 | 0 |

CAPTURE SITES, DECREASED THROUGHOUT THE SUMMER IN THE ALLOPATRIC REGION AS WATER BODIES DRIED UP. IN THE SYMPATRIC REGION, FLOODING IN THE SPRING OF 1974 INCREASED JULY MOISTURE LEVELS AT CAPTURE SITES. THIS EFFECT WAS NOT APPARENT UNTIL JULY BECAUSE THE FLOODING RESTRICTED SNAKE COLLECTION IN JUNE. THE EFFECT WAS MORE PRONOUNCED FOR T. RADIX THAN T. SIRTALIS BECAUSE THE PROPORTION OF T. SIRTALIS TAKEN IN THE SYMPATRIC REGION DURING THE SUMMER OF 1974 WAS SEVERELY REDUCED DUE TO DROWNING AT DENS IN THE SPRING. THIS PRODUCED SIGNIFICANT DIFFERENCES BETWEEN T. RADIX AND T. SIRTALIS IN THE SEASONAL TRENDS SHOWN BY MOISTURE WITHIN THE SYMPATRIC REGION, EVEN THOUGH THEIR INDIVIDUAL TRENDS WERE NOT SIGNIFICANT. LIGHT INTENSITY DECREASED THROUGHOUT THE SUMMER AS THE AZIMUTH OF THE SUN DECREASED. AIR AND SUBSTRATE TEMPERATURES PEAKED IN MID-SUMMER. TIME OF CAPTURE OF THE SNAKES, EXPRESSED AS A DEVIATION FROM MID-DAY, SHOWED NO SIGNIFICANT SEASONAL TRENDS.

UNIVARIATE COMPARISONS OF ENVIRONMENTAL FACTOR MEANS BETWEEN THE NICHES OF T. RADIX AND T. SIRTALIS, APPLIED TO ENVIRONMENTAL DATA THAT HAD NOT BEEN ADJUSTED FOR SEASONAL TRENDS, SHOWED HABITAT, MOISTURE, AIR TEMPERATURE AND SUBSTRATE TEMPERATURE TO BE MOST IMPORTANT.

ADJUSTMENT OF THE ENVIRONMENTAL DATA FOR SEASONAL TRENDS PRODUCED LITTLE EFFECT UPON THE FREQUENCY DISTRIBUTIONS OF ENVIRONMENTAL FACTORS (FIG. 5). DISCRIMINANT SCORES DERIVED FROM THESE DATA GAVE BETTER DISCRIMINATION BETWEEN THE NICHES OF T. RADIX AND T. SIRTALIS THAN DID ANY SINGLE ENVIRONMENTAL FACTOR, BOTH IN ALLOPATRIC AND IN SYMPATRIC REGIONS, BUT DID NOT GIVE ANY EVIDENCE OF NICHE DISPLACEMENT. ON THE CONTRARY, DISCRIMINANT SCORES BECAME MORE SIMILAR IN THE SYMPATRIC REGION THAN IN THE ALLOPATRIC REGION. MULTIVARIATE RESULTS AGREED WELL WITH THOSE DERIVED BY UNIVARIATE METHODS, ALTHOUGH SOME DIFFERENCES WERE

FIGURE 5. LOCATION OF T. RADIX AND T. SIRTALIS ON GRADIENTS OF THE SIX ENVIRONMENTAL FACTORS MEASURED AT CAPTURE SITES AFTER ADJUSTMENT OF ENVIRONMENTAL DATA FOR SEASONAL TRENDS. SYMBOLS AND FACTOR UNITS AS IN FIGURE 3. LOCATIONS OF BOTH SPECIES ON THE AXES OF THE DISCRIMINANT FUNCTIONS (DF) DERIVED FROM THE SEASONALLY ADJUSTED DATA ARE SHOWN BELOW.



APPARENT (TABLE 2). THE INDEX OF ECOLOGICAL IMPORTANCE, DERIVED FROM THE WEIGHTS IN THE DISCRIMINANT FUNCTION, WAS LARGE FOR HABITAT, BOTH IN ALLOPATRIC AND IN SYMPATRIC REGIONS, ALTHOUGH IT BECAME SMALLER IN THE SYMPATRIC REGION, INDICATING REDUCED IMPORTANCE THERE. THE NEGATIVE SIGN OF THIS INDEX INDICATES THAT T. RADIX OCCUPIED THE LOWER END OF THE HABITAT GRADIENT (PONDS) AND T. SIRTALIS THE UPPER END (CLOSED MARSHES). SUBSTRATE MOISTURE, IN CONTRAST TO UNIVARIATE RESULTS, WAS NOT ECOLOGICALLY IMPORTANT IN EITHER REGION. LIGHT INTENSITY WAS IMPORTANT ONLY IN THE SYMPATRIC REGION WHEREAS AIR TEMPERATURE WAS IMPORTANT ONLY IN THE ALLOPATRIC REGION, WITH T. RADIX OCCUPYING THE UPPER END OF THE GRADIENT IN BOTH CASES. SUBSTRATE TEMPERATURE WAS IMPORTANT IN BOTH ALLOPATRIC AND SYMPATRIC REGIONS, ALTHOUGH IT BECAME MORE IMPORTANT IN THE LATTER REGION. ASSOCIATED WITH THE INCREASED IMPORTANCE OF THIS FACTOR IN THE SYMPATRIC REGION, IN CONTRAST TO UNIVARIATE RESULTS, WAS A REVERSAL IN THE RELATIVE SPECIES POSITIONS ON THE GRADIENT, T. RADIX COMING TO OCCUPY THE UPPER RATHER THAN THE LOWER END. TIME OF CAPTURE, EXPRESSED AS A DEVIATION FROM MID-DAY, WAS NOT AN ECOLOGICALLY IMPORTANT FACTOR IN EITHER THE ALLOPATRIC OR THE SYMPATRIC REGION. THESE RESULTS AGREE WITH THOSE BASED ON UNIVARIATE COMPARISONS, ALTHOUGH IN THE SYMPATRIC REGION THEY GIVE CONSIDERABLY LESS IMPORTANCE TO THE TIME FACTOR.

DAILY TEMPERATURE PROFILES DERIVED FROM RECORDINGS AT THE STATIONS SET UP IN THE CLOSED MARSH, ADJACENT ASPEN FOREST, POND AND ADJACENT MEADOW, SHOWED THAT THE CLOSED MARSH HABITAT CLASS AND THE FOREST WITH WHICH IT TENDS TO BE ASSOCIATED EXHIBITED GREATER DIFFERENCES BETWEEN AIR AND SUBSTRATE TEMPERATURE THAN DID THE POND HABITAT CLASS AND THE MEADOW WITH WHICH IT TENDS TO BE ASSOCIATED. THESE PROFILES WERE

TABLE 2. DISCRIMINANT FUNCTION COEFFICIENTS AND INDICES OF DISCRIMINATING VALUE DERIVED FROM THEM IN ALLOPATRIC AND SYMPATRIC REGIONS

| ALLOPATRIC | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME | R_c^2 * |
|-------------|---------|----------|-------|-----------|------------|--------|-----------|
| COEFFICIENT | -30.729 | -2.922 | 2.021 | 1.110 | -1.227 | -1.703 | .54 |
| INDEX | - .502 | - .066 | .085 | .117 | - .103 | - .069 | |
| SYMPATRIC | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME | R_c^2 * |
| COEFFICIENT | - 6.117 | -0.243 | 1.660 | - 0.105 | 0.577 | -0.661 | .25 |
| INDEX | - .163 | - .010 | .142 | - .022 | .104 | - .055 | |

* R_c^2 = SQUARED CANNONICAL CORRELATION COEFFICIENT (FRACTION OF VARIATION IN SPECIES MEMBERSHIP ACCOUNTED FOR BY THE DISCRIMINANT FUNCTION)

PARTICULARLY SENSITIVE TO VARIATIONS IN CLOUD COVER AND WIND VELOCITY. SAMPLE PROFILES FROM TEMPERATURES TAKEN ON 25 JULY, 1974, AN UNUSUALLY STILL AND WARM DAY WITH NO CLOUD COVER, ARE SHOWN IN FIGURE 6.

SUBSTRATE MOISTURE AT CAPTURE SITES PROVED TO BE HIGHLY CORRELATED WITH SUBSTRATE TEMPERATURE. THIS WAS PARTICULARLY TRUE WITHIN THE INTERLAKE RANGE OF T. SIRTALIS ($r = 0.94$).

THERMAL RELATIONS

ORAL AND CLOACAL TEMPERATURES OF T. RADIX WERE SIGNIFICANTLY HIGHER ($P < .01$) THAN THOSE OF T. SIRTALIS IN THE ALLOPATRIC REGION ONLY. BODY TEMPERATURES OF T. SIRTALIS INCREASED SIGNIFICANTLY (ORAL $P < .05$); CLOACAL $P < .01$) IN THE SYMPATRIC REGION. FREQUENCY DISTRIBUTIONS OF BODY TEMPERATURES WERE NEGATIVELY SKEWED (FIG. 7).

MULTIPLE REGRESSION SHOWED ORAL TEMPERATURES OF T. RADIX TO DEPEND MOST STRONGLY UPON LIGHT INTENSITY, AIR TEMPERATURE AND SUBSTRATE TEMPERATURE (FIG. 8). CLOACAL TEMPERATURES OF T. RADIX DEPENDED MOST STRONGLY UPON THE SAME THREE ENVIRONMENTAL FACTORS. OF THESE THREE FACTORS AIR TEMPERATURE WAS MOST IMPORTANT. ORAL TEMPERATURES OF T. SIRTALIS ALSO DEPENDED MOST STRONGLY UPON LIGHT INTENSITY, AIR TEMPERATURE AND SUBSTRATE TEMPERATURE. HABITAT EXERTED AN ADDITIONAL EFFECT UPON ORAL TEMPERATURES OF T. SIRTALIS, OVER AND ABOVE THAT PRODUCED BY THE OTHER ENVIRONMENTAL FACTORS, ORAL TEMPERATURES BEING LOWER IN THE CLOSED MARSH. CLOACAL TEMPERATURES OF T. SIRTALIS DEPENDED MOST STRONGLY UPON AIR TEMPERATURE AND SUBSTRATE TEMPERATURE AND WERE INDEPENDENT OF LIGHT INTENSITY. CLOACAL TEMPERATURES, LIKE ORAL TEMPERATURES, WERE LOWER IN THE CLOSED MARSH, OTHER ENVIRONMENTAL FACTORS BEING EQUAL. AN ADDITIONAL EFFECT SEEMED TO BE EXERTED UPON THE CLOACAL TEMPERATURES OF

**FIGURE 6. SAMPLE DAILY TEMPERATURE PROFILES DERIVED FROM
RECORDINGS AT STATIONS LOCATED IN CLOSED MARSH, ASPEN FOREST,
POND, AND MEADOW.**

FIGURE 7. RELATIVE FREQUENCY DISTRIBUTIONS OF ORAL AND CLOACAL TEMPERATURES FOR T. RADIX AND T. SIRTALIS IN ALLOPATRIC AND SYMPATRIC REGIONS. THE MEAN TEMPERATURE IS INDICATED BY AN ARROW (†).

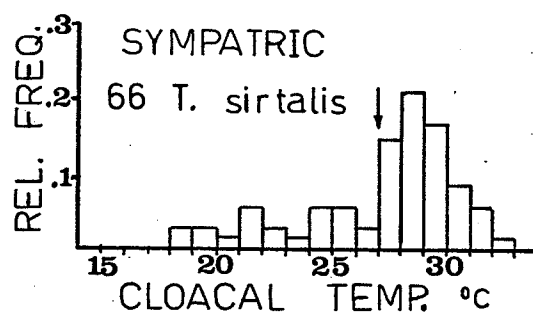
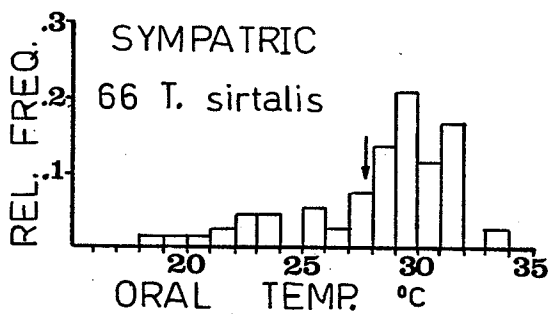
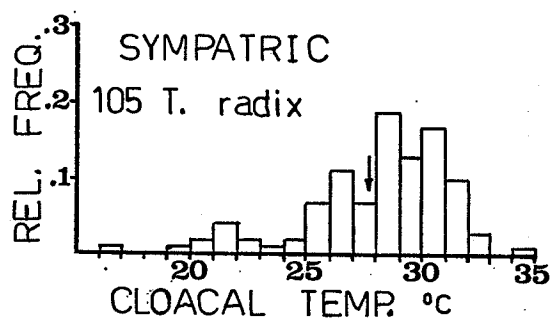
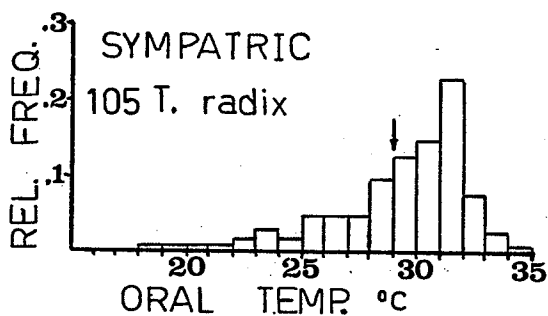
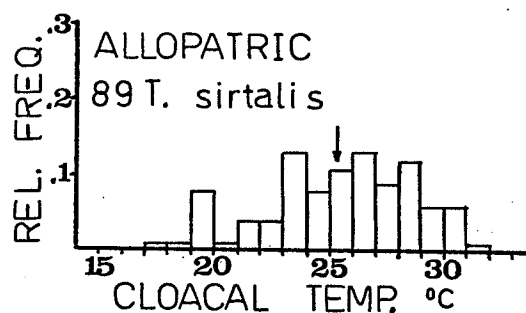
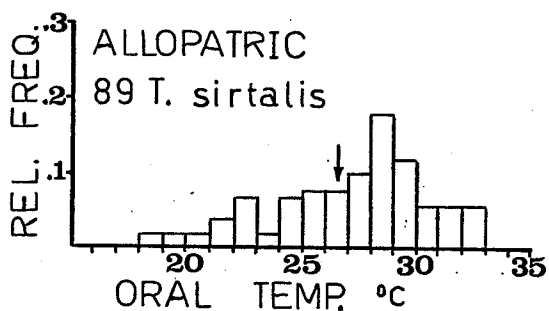
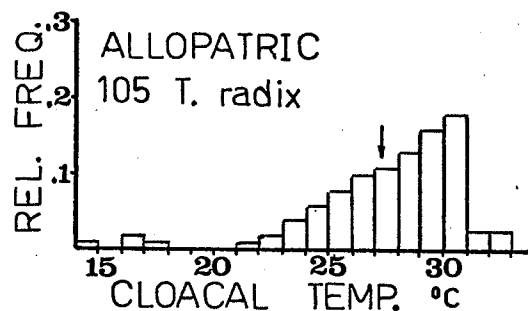
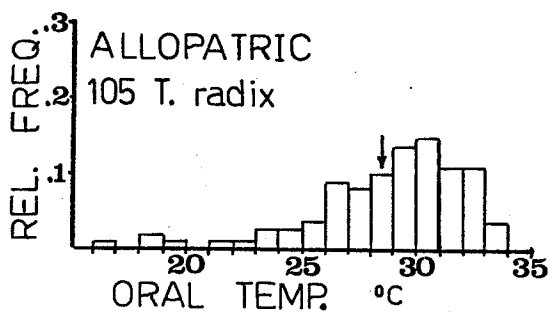
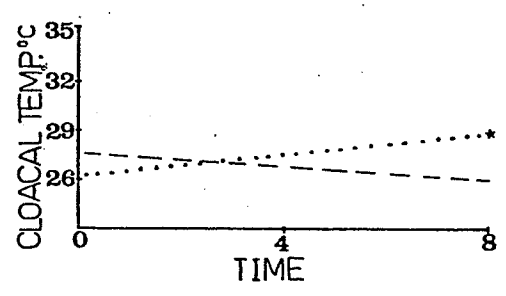
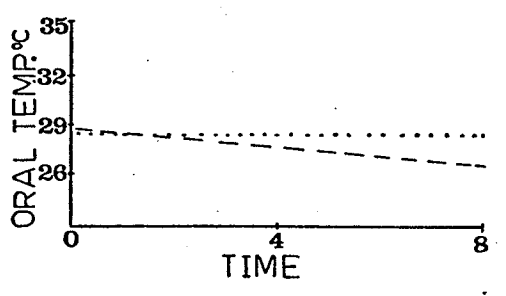
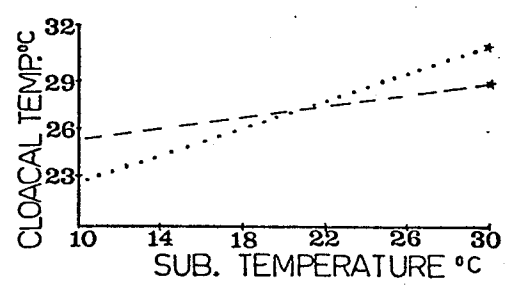
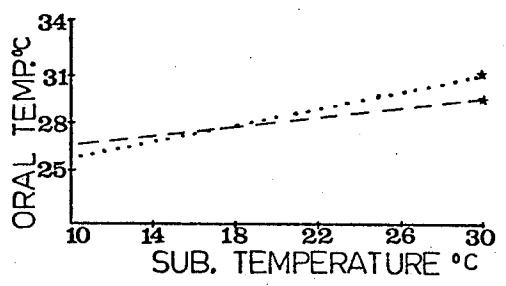
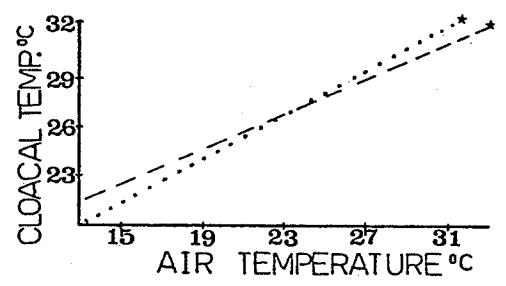
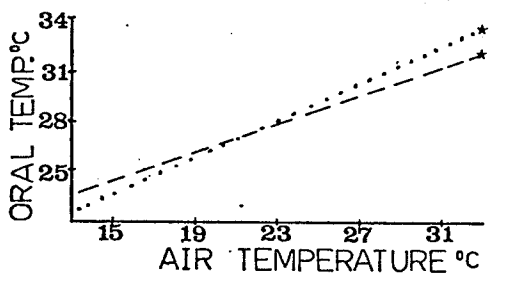
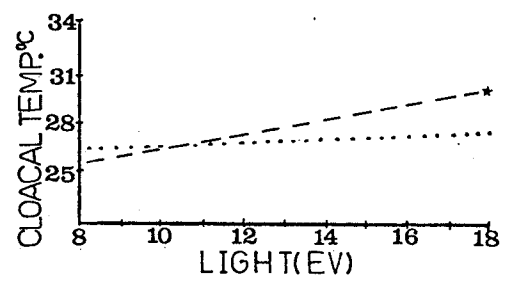
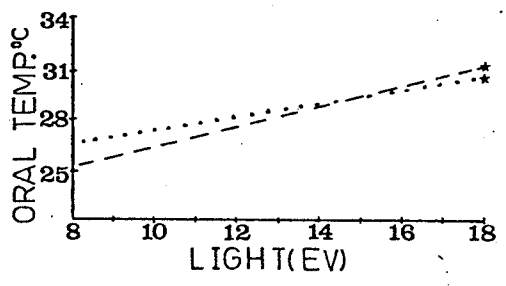
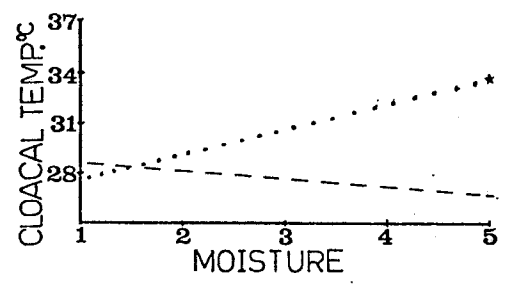
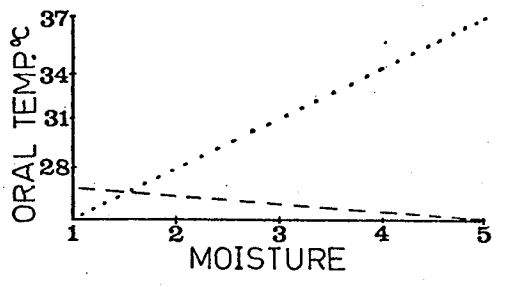
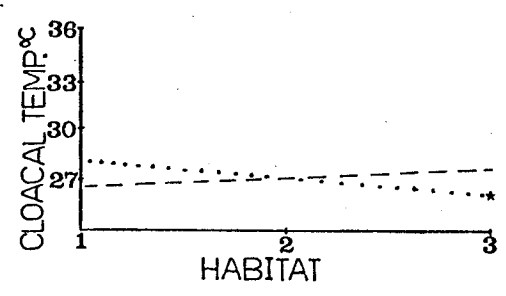
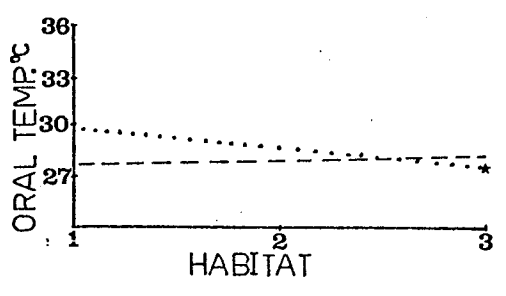


FIGURE 8. PARTIAL REGRESSION OF ORAL AND CLOACAL TEMPERATURES ON EACH OF THE SIX ENVIRONMENTAL FACTORS MEASURED AT CAPTURE SITES FOR I. RADIX (----) AND I. SIRTALIS (.....). FACTOR UNITS AS IN FIGURE 3. SIGNIFICANT PARTIAL REGRESSIONS ($P < .01$) ARE INDICATED BY A STAR (*).



T. SIRTALIS BY SUBSTRATE MOISTURE AND TIME OF CAPTURE, CLOACAL TEMPERATURES BEING HIGHER AT MOIST CAPTURE SITES AND LOWER NEAR MID-DAY, OTHER FACTORS BEING EQUAL. THE RELATIONSHIPS OF ORAL AND CLOACAL TEMPERATURE TO THE HABITAT FACTOR DIFFERED SIGNIFICANTLY ($P < .01$) BETWEEN T. RADIX AND T. SIRTALIS, BEING NEGATIVE FOR T. SIRTALIS ONLY. THE RELATIONSHIPS OF CLOACAL TEMPERATURE TO SUBSTRATE MOISTURE, SUBSTRATE TEMPERATURE AND TIME OF CAPTURE DIFFERED SIGNIFICANTLY ($P < .01$) BETWEEN T. RADIX AND T. SIRTALIS, BEING MORE POSITIVE FOR T. SIRTALIS.

ANALYSIS OF THE WARMING RATES FOR T. RADIX AND T. SIRTALIS UNDER RADIANT ENERGY IN THE LABORATORY SHOWED HIGHLY SIGNIFICANT INTERACTION ($P < .01$) BETWEEN THE SPECIES AND STATE EFFECTS (TABLE 3). THE DIFFERENCE IN WARMING RATES BETWEEN SPECIES DEPENDED STRONGLY UPON WHETHER THE SNAKES WERE ALIVE OR DEAD. THIS MADE INTERPRETATION OF THE MAIN EFFECTS, DUE TO SPECIES OR STATES ALONE, DIFFICULT. THE INTERACTION SEEMED TO BE DUE TO A DIFFERENCE IN THE ESCAPE BEHAVIOR OF LIVING SNAKES, T. SIRTALIS WRITHING MORE VIGOROUSLY IN THE HEATING CHAMBER AND FREQUENTLY TURNING BELLY UP IN AN EFFORT TO RID ITSELF OF THE THERMOMETER PROBE. T. RADIX BEHAVED MORE SEDATELY, ESPECIALLY AT THE BEGINNING OF EACH EXPERIMENT BEFORE IT HAD WARMED UP. WHETHER THIS WAS DUE TO THERMAL INHIBITION OF MOTOR ACTIVITY OR TO A MORE DOCILE TEMPERMENT MORE TIME WAS SPENT IN A POSTURE CONDUCTIVE TO BASKING. TO EXAMINE SPECIES DIFFERENCES IN WARMING RATE IN THE ABSENCE OF INTERACTION, THE FACTORIAL DESIGN WAS ABANDONED, AND THE DATA FROM DEAD SNAKES ONLY WERE REANALYZED. THAMNOPHIS SIRTALIS SHOWED A SIGNIFICANTLY HIGHER ($P < .01$) RATE OF ABSORBING RADIANT ENERGY THAN T. RADIX BEFORE VARIABILITY IN RATES DUE TO TOTAL LENGTH OR VISUAL ALBEDO HAD BEEN REMOVED. VARIABILITY IN WARMING RATES WITH TOTAL LENGTH

TABLE 3. ANALYSIS OF COVARIANCE FOR WARMING RATES

| <u>TWO-WAY DESIGN</u> | | | | |
|--|-----------|-----------|-----------|----------|
| <u>STEP 1 (LENGTH ADJUSTED)</u> | | | | |
| <u>SOURCE</u> | <u>df</u> | <u>SS</u> | <u>MS</u> | <u>F</u> |
| SPECIES | 1 | 6.500 | 6.500 | 13.67* |
| STATES | 1 | 0.535 | 0.535 | 1.13 |
| INTERACTION | 1 | 7.468 | 7.468 | 15.71* |
| ERROR | 75 | 35.656 | 0.476 | |
| <u>STEP 2 (LENGTH AND ALBEDO ADJUSTED)</u> | | | | |
| <u>SOURCE</u> | <u>df</u> | <u>SS</u> | <u>MS</u> | <u>F</u> |
| SPECIES | 1 | 0.742 | 0.742 | 1.62 |
| STATES | 1 | 0.138 | 0.138 | 0.30 |
| INTERACTION | 1 | 7.309 | 7.309 | 10.83* |
| ERROR | 74 | 33.882 | 0.458 | |
| <u>ONE-WAY DESIGN</u> | | | | |
| <u>STEP 1 (LENGTH ADJUSTED)</u> | | | | |
| <u>SOURCE</u> | <u>df</u> | <u>SS</u> | <u>MS</u> | <u>F</u> |
| SPECIES | 1 | 12.698 | 12.698 | 43.888* |
| ERROR | 37 | 10.705 | 0.289 | |
| <u>STEP 2 (LENGTH AND ALBEDO ADJUSTED)</u> | | | | |
| <u>SOURCE</u> | <u>df</u> | <u>SS</u> | <u>MS</u> | <u>F</u> |
| SPECIES | 1 | 3.097 | 3.097 | 11.967* |
| ERROR | 36 | 9.317 | 0.259 | |

* F SIGNIFICANT (P < .01)

OF THE SNAKE DIFFERED SIGNIFICANTLY ($.005 < P < .01$) BETWEEN I. RADIX AND I. SIRTALIS, RATES DEPENDING MORE STRONGLY UPON TOTAL LENGTH FOR I. SIRTALIS. NEVERTHELESS, A COMMON RELATIONSHIP BETWEEN WARMING RATE AND TOTAL LENGTH WAS USED TO REMOVE VARIABILITY IN RATES DUE TO LENGTH. THIS SERVED TO INCREASE THE DIFFERENCES BETWEEN WARMING RATES OF I. RADIX AND I. SIRTALIS, BUT WAS SOMEWHAT ARTIFICIAL SINCE RATE-LENGTH RELATIONSHIPS IN I. RADIX AND I. SIRTALIS PROBABLY DIFFERED. REMOVAL OF ADDITIONAL VARIABILITY IN WARMING RATES DUE TO VISUAL ALBEDO, ALTHOUGH IT REDUCED THE DIFFERENCE BETWEEN SPECIES IN RATES OF WARMING, DID NOT REDUCE THE RATE DIFFERENCE TO INSIGNIFICANCE (FIG. 9). THE RELATIONSHIP BETWEEN WARMING RATE AND VISUAL ALBEDO, AS IT WAS MEASURED IN THIS EXPERIMENT AT A SINGLE POINT ON THE DORSAL SURFACE OF THE SNAKE, WAS POOR FOR BOTH I. RADIX AND I. SIRTALIS ($.15 > P > .10$) AND DID NOT DIFFER BETWEEN SPECIES ($P > .01$).

DIFFERENCES IN VISUAL ALBEDO BETWEEN I. RADIX AND I. SIRTALIS WERE GREATEST ALONG THE EDGES OF THE VENTRAL SCUTES (BELOW THE HORIZONTAL) AND IN THE REGION OF THE LATERAL STRIPES (30° ABOVE THE HORIZONTAL), I. RADIX HAVING A GREATER VISUAL ALBEDO THAN I. SIRTALIS (FIG. 10). SIMILAR DIFFERENCES WERE SOMEWHAT OBSCURED OVER THE REGION OF THE DORSAL STRIPE (90° ABOVE HORIZONTAL) BY A SHADOWING EFFECT FROM THE LIGHT METER.

ACTIVITY

A BIMODAL PATTERN OF DAILY ACTIVITY WAS SUGGESTED BY DAILY PROFILES OF CATCH PER SEARCH HOUR IN THE FIELD FOR BOTH I. RADIX AND I. SIRTALIS IN THE ALLOPATRIC REGION (FIG. 11). EFFORT IN THIS REGION RANGED FROM 3 TO 22 SEARCH HOURS PER HOURLY TIME INTERVAL. IN THE SYMPATRIC REGION THE MORNING AND EVENING PEAKS OF ACTIVITY FOR I. SIRTALIS WERE FARTHER APART

FIGURE 9. MEAN WARMING RATES (° C/MIN 10^{-2}) OF I. RADIX ALIVE (RA) AND DEAD (RD) AND OF I. SIRTALIS ALIVE (SA) AND DEAD (SD) UNDER A RADIANT ENERGY SOURCE AT 10° C. WARMING RATES OF DEAD SNAKES ARE SHOWN AFTER ADJUSTMENT FOR TOTAL LENGTH ONLY AND AFTER ADJUSTMENT FOR BOTH TOTAL LENGTH AND ALBEDO. REGRESSIONS OF WARMING RATE ON THESE COVARIATES ARE SHOWN FOR DEAD I. RADIX AND DEAD I. SIRTALIS. SIGNIFICANT REGRESSIONS ($P < .01$) ARE INDICATED BY A STAR (*).

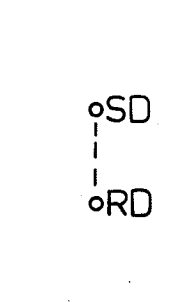
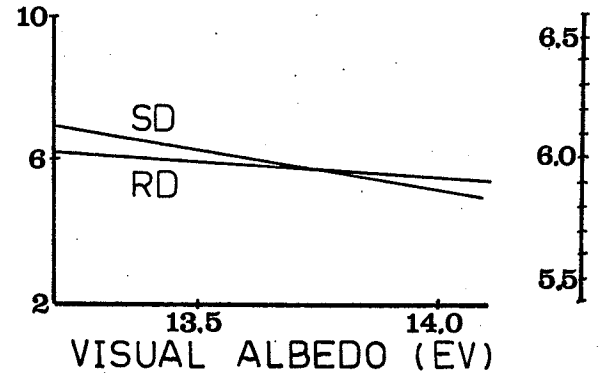
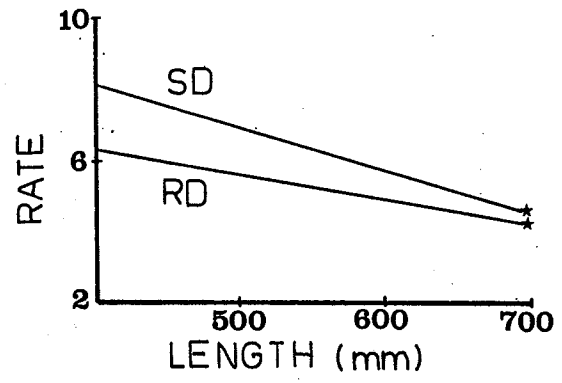
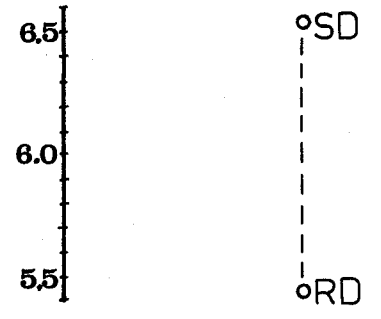
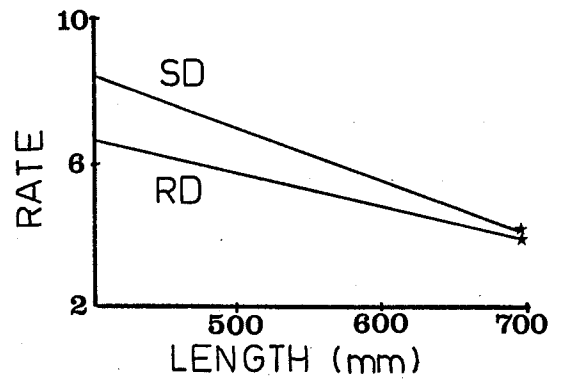
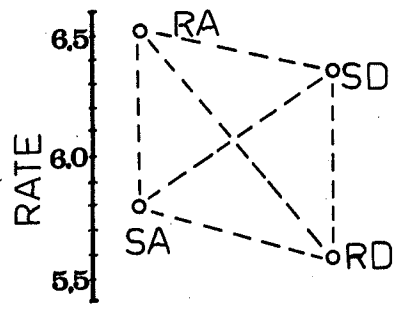


FIGURE 10. POINT REFLECTANCE AROUND THE BODY CIRCUMFERENCE OF SNAKES. OPEN CIRCLES (O) SHOW SAMPLE VALUES OF REFLECTANCE AT POINTS ON THE CIRCUMFERENCE OF THE EMPTY GLASS TUBING WHICH WAS USED TO CONFINE SNAKES FOR EXAMINATION. SOLID SYMBOLS WITH 95% CONFIDENCE INTERVALS SHOW MEAN VALUES OF REFLECTANCE AT POINTS ON THE CIRCUMFERENCE OF SNAKES WITHIN THE GLASS TUBING. THIRTY I. RADIX (ϕ) AND 27 I. SIRTALIS (\star) WERE EXAMINED.

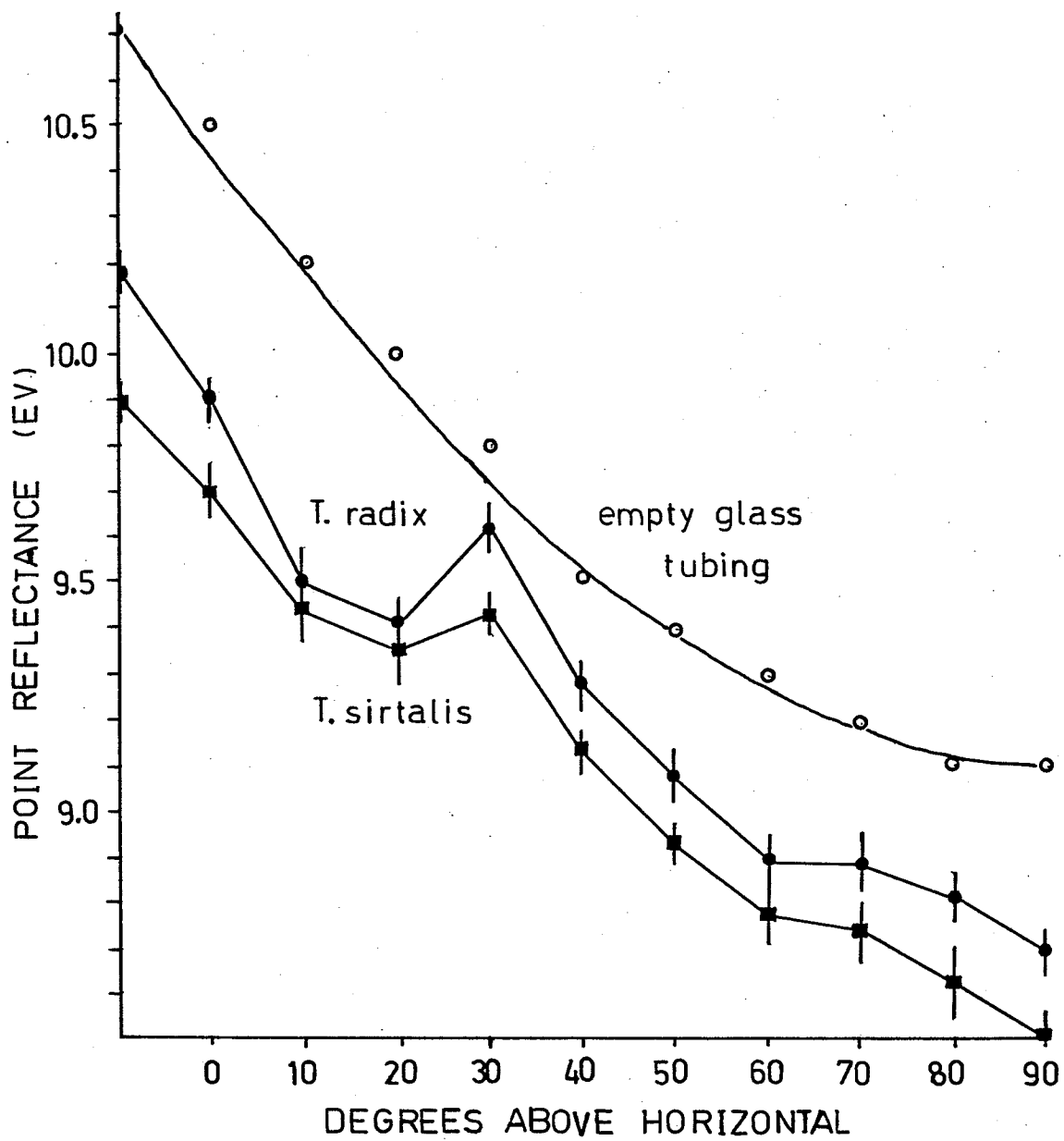
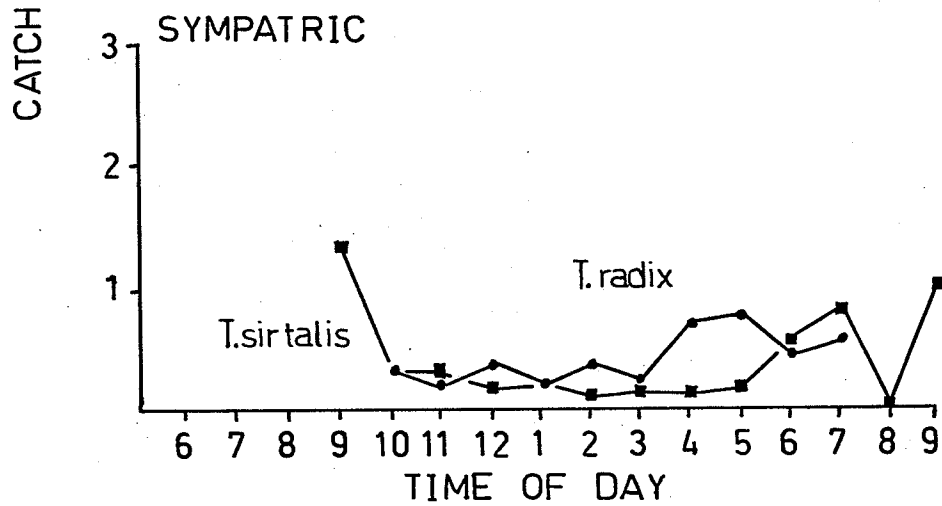
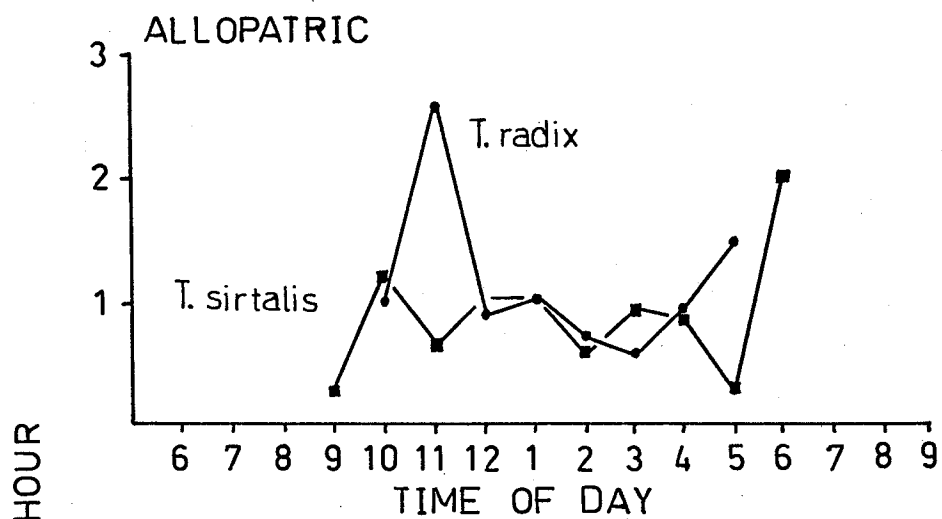


FIGURE 11. PROFILES OF CATCH PER SEARCH-HOUR CALCULATED FOR HOURLY INTERVALS THROUGHOUT THE COURSE OF THE DAY. PROFILES ARE SHOWN FOR T. RADIX (•) AND T. SIRTALIS (■) IN ALLOPATRIC AND SYMPATRIC REGIONS.



THAN IN THE ALLOPATRIC REGION, WHILE T. RADIX ELIMINATED ITS MORNING PEAK AND BECAME MORE ACTIVE TOWARDS MID-DAY. EFFORT IN THIS REGION RANGED FROM 4 TO 41 SEARCH HOURS PER HOURLY INTERVAL AND CATCHES WERE GENERALLY LOWER FOR BOTH SPECIES THAN IN THE ALLOPATRIC REGION.

A BIMODAL PATTERN OF DAILY ACTIVITY WAS ALSO SUGGESTED IN THE LABORATORY, UNDER CONTROLLED TEMPERATURE AND LIGHT REGIMES, BY BOTH T. RADIX (FIG. 12) AND T. SIRTALIS (FIG. 13). THE TIME BETWEEN ACTIVITY PEAKS WAS GREATEST AT HIGHER TEMPERATURES FOR BOTH SPECIES. ALTHOUGH LARGE CONFIDENCE INTERVALS MAKE EXACT DESCRIPTION OF THE TEMPERATURE EFFECT DIFFICULT, THE CHANGE IN ACTIVITY PATTERN WITH A TEMPERATURE CHANGE APPEARED TO BE GREATEST AT LOW TEMPERATURES FOR T. RADIX AND GREATEST AT HIGH TEMPERATURES FOR T. SIRTALIS. THAMNOPHIS SIRTALIS USED THE WATER AS A COOLANT AT HIGH TEMPERATURE MUCH MORE READILY THAN DID T. RADIX.

FIGURE 12. ACTIVITY PROFILES FOR I. RADIX THROUGHOUT THE COURSE OF THE DAY UNDER CONTROLLED LIGHT AND TEMPERATURE REGIMES. LIGHT AND TEMPERATURE REGIMES ARE SHOWN ABOVE EACH GRAPH. VARIATION IN THE INTENSITY OF STIPLING SHOWS THE VARIATION OF LIGHT INTENSITY IN FIVE EQUAL STEPS BETWEEN MAXIMUM INTENSITY AND COMPLETE DARKNESS. TEMPERATURE CHANGES BEGAN AT THE TIMES INDICATED BUT TOOK APPROXIMATELY TWO HOURS TO REACH COMPLETION. NINETY-FIVE PERCENT CONFIDENCE INTERVALS ARE SHOWN ON THE MEAN NUMBER OF SNAKES EXPOSED AT EACH TIME OF DAY ($n = 6$ DAYS). SOLID CIRCLES (•) WITHOUT CONFIDENCE INTERVALS SHOW THE NUMBER EXPOSED IN THE OPEN AS OPPOSED TO THE SHADE AND X SHOWS THE NUMBER OF THESE EXPOSED IN THE WATER.

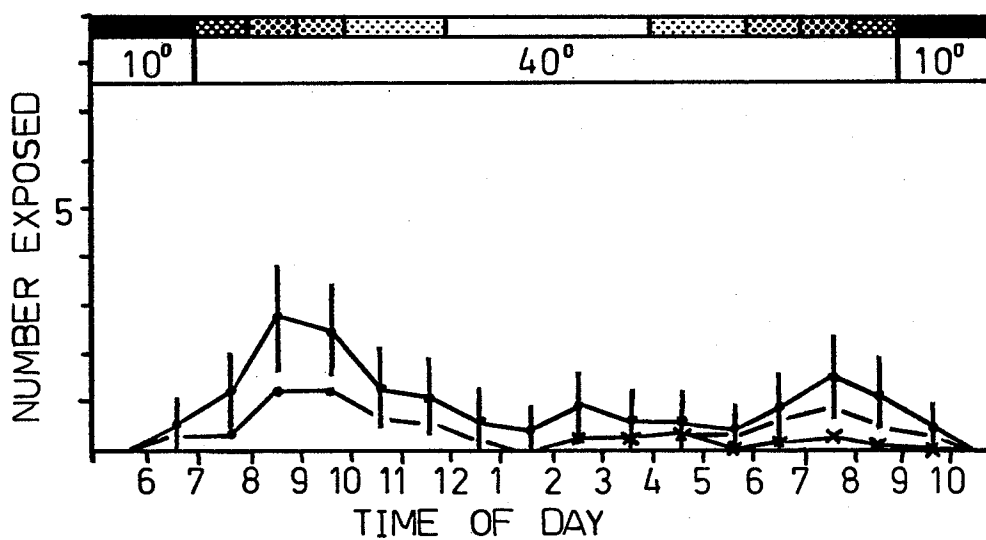
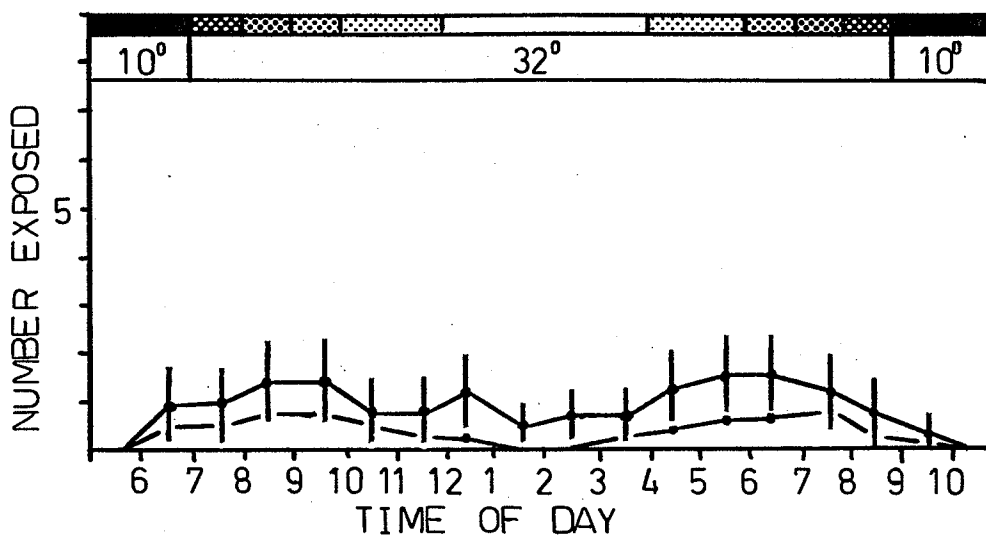
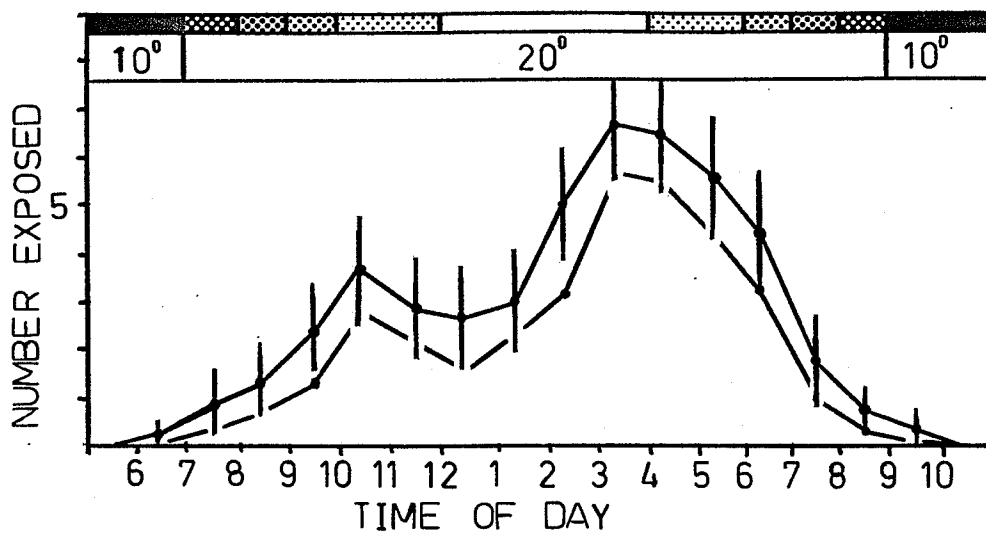
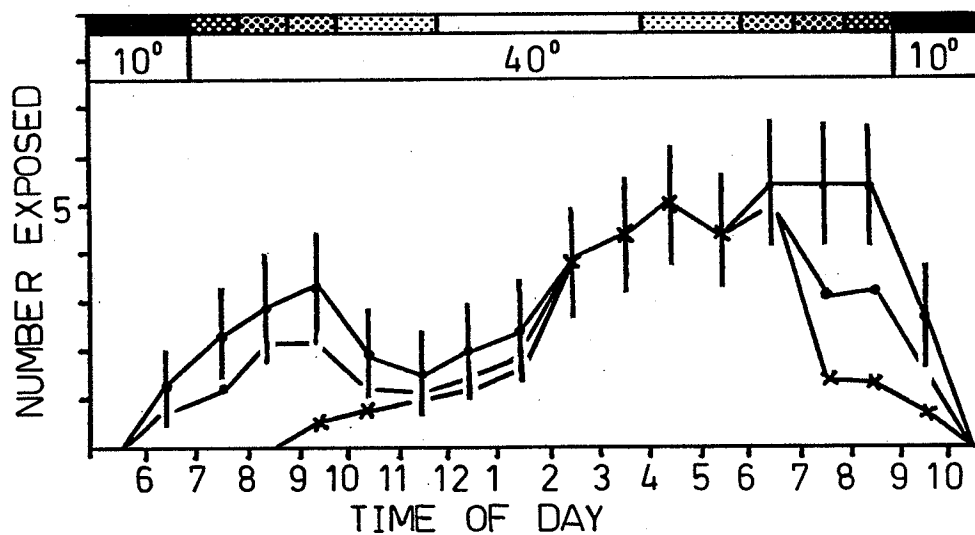
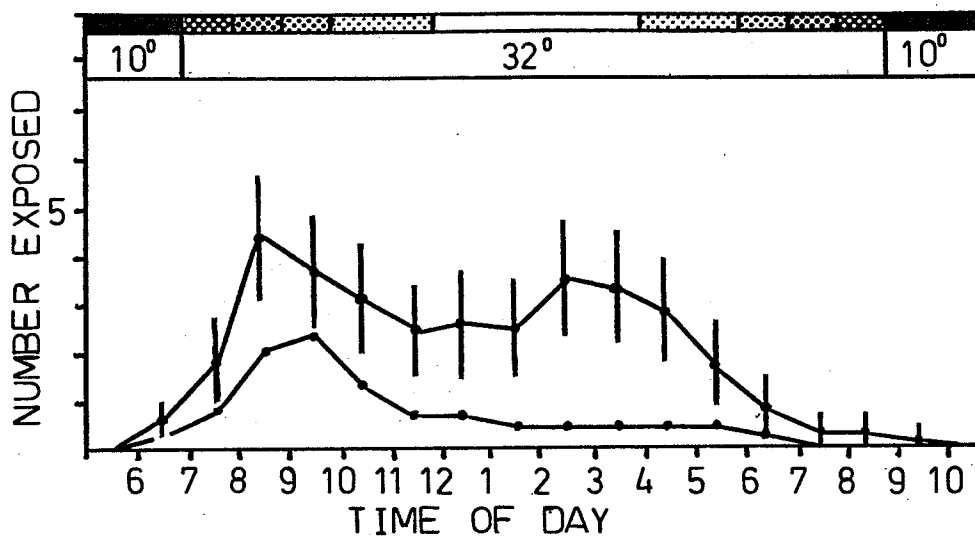
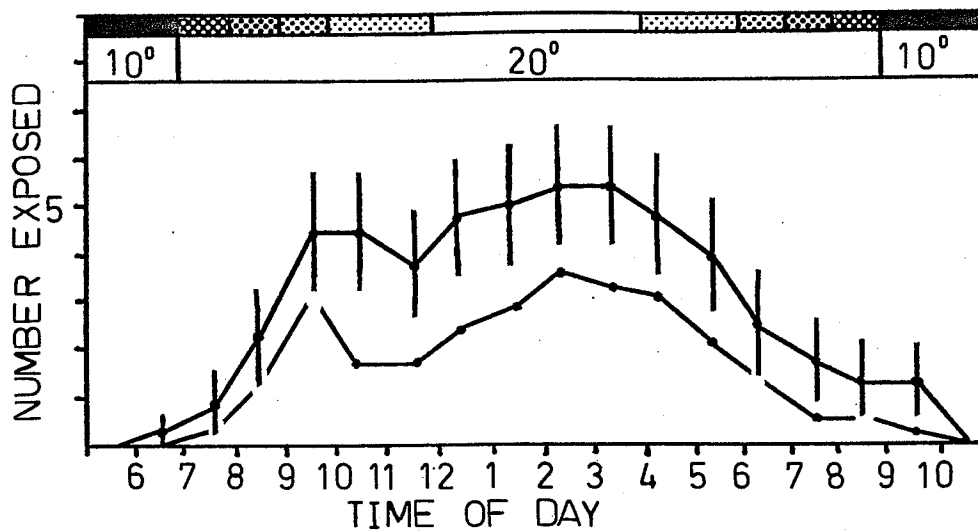


FIGURE 13. ACTIVITY PROFILES FOR I. SIRTALIS THROUGHOUT THE
COURSE OF THE DAY UNDER CONTROLLED LIGHT AND TEMPERATURE REGIMES.
SYMBOLS AS IN FIGURE 11.



DISCUSSION

FEEDING HABITS

BOTH T. RADIX AND T. SIRTALIS APPEARED TO FEED OPPORTUNISTICALLY, TAKING A WIDE VARIETY OF FOOD ITEMS IN ROUGH PROPORTION TO THEIR APPARENT ABUNDANCE. THIS WAS PROBABLY AN ADAPTATION TO THE SHORT GROWING SEASON ENCOUNTERED IN THE TEMPERATE ZONE. IN CONTRAST TO THE STUDIES OF CARPENTER (1952), FOUQUETTE (1954) AND FLEHARTY (1967), WHO WORKED WITH DIFFERENT SPECIES COMBINATIONS, NO DIFFERENCES WERE FOUND BETWEEN THE FEEDING HABITS OF T. RADIX AND T. SIRTALIS IN SYMPATRY. ALTHOUGH T. SIRTALIS ALTERED ITS FEEDING HABITS IN THE SYMPATRIC REGION, IT DID NOT DO SO IN SUCH A WAY AS TO DISPLACE ITS NICHE FROM THAT OF T. RADIX. THE MAJOR CHANGES INVOLVED AN INCREASED UTILIZATION OF WOOD FROGS AND A DECREASED UTILIZATION OF CHORUS FROGS. THESE CHANGES MAY HAVE BEEN THE RESULT OF CHANGES IN THE RELATIVE AVAILABILITY OF WOOD FROGS AND CHORUS FROGS. SINCE THERE WAS NO NICHE DISPLACEMENT IN SYMPATRY WITH RESPECT TO FEEDING HABITS, THE CHANGES CANNOT BE ATTRIBUTED TO SPECIES INTERACTION. WHITE AND KLOB (1974), IN THEIR STUDY OF TWO GARTER SNAKE SPECIES IN CALIFORNIA, SIMILARLY REJECTED THE HYPOTHESIS OF COMPETITIVE DISPLACEMENT SINCE CHANGES IN THE FEEDING HABITS OF T. SIRTALIS FITCHI, WHEN IN SYMPATRY WITH T. ELEGANS, WERE NOT IN THE DIRECTION OF NICHE DISPLACEMENT. THEY FELT THAT FEEDING HABITS WERE DETERMINED LARGELY BY AVAILABILITY AS APPEARED TO BE THE CASE IN THE PRESENT STUDY.

ENVIRONMENTAL FACTORS

IN THE ALLOPATRIC REGION, HABITAT, AIR TEMPERATURE AND SUBSTRATE TEMPERATURE CONTRIBUTED MOST STRONGLY TO NICHE DISCRIMINATION (TABLE 2). ALTHOUGH UNIVARIATE COMPARISONS BETWEEN T. RADIX AND T. SIRTALIS ALSO ATTRIBUTED IMPORTANCE TO SUBSTRATE MOISTURE, MULTIVARIATE RESULTS INDICATED THAT THIS FACTOR WAS REDUNDANT. ITS STRONG CORRELATION WITH SUBSTRATE TEMPERATURE EXPLAINS THIS REDUNDANCY.

THE ECOLOGICAL IMPORTANCE OF HABITAT CAN BE RELATED TO THE THERMAL RELATIONS OF THE SNAKES. HABITAT EXERTED AN INDEPENDENT EFFECT UPON BOTH ORAL AND CLOACAL TEMPERATURES OF T. SIRTALIS; THIS WAS PROBABLY DUE TO THE SHADE PROVIDED BY THE SEDGE MAT IN THE CLOSED MARSH. THE CLOSED MARSH AND ASSOCIATED ASPEN FOREST OFFERED A WIDE RANGE OF ENVIRONMENTAL TEMPERATURES TO THE SNAKES; THIS IS PROBABLY IMPORTANT TO A SPECIES SUCH AS T. SIRTALIS THAT ABSORBS RADIANT ENERGY QUICKLY. ASPECTS OF HABITAT RELEVANT TO BEHAVIORAL TEMPERATURE CONTROL WERE SIMILARLY IMPORTANT TO NICHE DISCRIMINATION IN THE STUDIES OF CARPENTER (1952) AND FLEHARTY (1967).

THE IMPORTANCE OF AIR AND SUBSTRATE TEMPERATURE TO NICHE DISCRIMINATION IN THE ALLOPATRIC REGION CAN ALSO BE RELATED TO THE THERMAL RELATIONS OF THE SNAKES. BOTH FACTORS EXERTED A STRONG EFFECT UPON ORAL AND CLOACAL TEMPERATURES OF T. RADIX AND T. SIRTALIS. SINCE T. RADIX HAD A HIGHER VISUAL ALBEDO THAN T. SIRTALIS OVER MUCH OF ITS BODY SURFACE, IT WAS PROBABLY BETTER ADAPTED TO THE HIGHER AIR TEMPERATURES THAT CHARACTERIZED ITS RANGE AND IT WAS ABLE TO TOLERATE THEM BY SEEKING OUT LOW SUBSTRATE TEMPERATURES. THAMNOPHIS SIRTALIS WAS APPARENTLY UNABLE TO TOLERATE HIGH AIR TEMPERATURES WITHOUT A THERMAL REFUGE IN THE FORM OF CLOSED MARSH OR ASPEN FOREST AND, PROBABLY FOR THIS REASON, IT DID

ERRATA

Hart, D.R., 1975. A quantitative niche comparison of the Western Plains Garter Snake (Thamnophis radix haydeni) and the Red-Sided Garter Snake (Thamnophis sirtalis parietalis) in allopatric and sympatric regions of Manitoba's Interlake District. MSc. Thesis, University of Manitoba.

Page 56. An important phrase has been omitted and should be inserted between lines 13 and 14 as follows:

line 13region
and T. sirtalis seeking out lower light
intensities and substrate temperatures to
compensate for higher available air tem-
peratures in the sympatric region

line 14 and.....

NOT OCCUR MUCH BEYOND THE RANGE OF THESE HABITAT TYPES. FLEHARTY (1967) SIMILARLY FOUND AIR AND SUBSTRATE TEMPERATURES TO BE USEFUL IN DEFINING THE NICHEs OF CARTER SNAKE SPECIES.

IN THE RESTRICTED SYMPATRIC REGION, THE AVAILABLE RANGE OF ENVIRONMENTAL FACTORS WAS PROBABLY REDUCED. AS A RESULT, THE IMPORTANCE OF HABITAT AND AIR TEMPERATURE TO NICHE DISCRIMINATION WAS ALSO REDUCED, THE LATTER BECOMING INSIGNIFICANT. HOWEVER, THE IMPORTANCE OF SUBSTRATE TEMPERATURE AND LIGHT INTENSITY AT CAPTURE SITES WAS INCREASED (TABLE 2). THIS CAN ONLY BE INTERPRETED AS A BEHAVIORAL REACTION OF THE SNAKES, BUT NEED NOT BE EXPLAINED AS A REACTION TO THE PRESENCE OF ANOTHER SPECIES. IT MAY REPRESENT COMPENSATION FOR CHANGES IN THE AVAILABLE NICHE, I. RADIX SEEKING OUT HIGHER LIGHT INTENSITIES AND SUBSTRATE TEMPERATURES TO COMPENSATE FOR LOWER AVAILABLE AIR TEMPERATURES IN THE SYMPATRIC REGION AND FOR THE SCARCITY OF SHADE NORMALLY AFFORDED BY THE CLOSED MARSH AND FOREST OF ITS ALLOPATRIC HABITAT.

ONE OF THE WAYS IN WHICH THIS SELECTION WAS ACCOMPLISHED IS SUGGESTED BY THE DAILY PROFILES OF CATCH PER SEARCH HOUR. IN THE ALLOPATRIC REGION, BOTH SPECIES SHOWED A ROUGHLY BIMODAL ACTIVITY PATTERN WITH MORNING AND EVENING PEAKS. IN THE SYMPATRIC REGION, HOWEVER, I. RADIX WAS MOST ACTIVE DURING MID-AFTERNOON CLOSE TO THE HOTTEST PART OF THE DAY, AND I. SIRTALIS WAS ACTIVE EARLIER IN THE MORNING AND LATER IN THE EVENING, APPARENTLY AVOIDING THE HEAT OF MID-AFTERNOON. THIS INCREASED DIFFERENCE BETWEEN THE ACTIVITY PATTERNS OF I. RADIX AND I. SIRTALIS IN THE SYMPATRIC REGION WAS ILLUSTRATED BY UNIVARIATE COMPARISONS OF TIME OF CAPTURE, CODED TO REFLECT BIMODALITY OF ACTIVITY. THE DIFFERENCE IN THIS FACTOR BETWEEN I. RADIX AND I. SIRTALIS WAS INCREASED IN THE SYMPATRIC REGION, BUT WAS NOT STRONG ($.05 > P > .01$). MULTIVARIATE RESULTS VIRTUALLY ELIMINATED THIS INCREASE IN IMPORTANCE IN THE SYMPATRIC

REGION INDICATING THAT THE ACTIVITY SHIFT WAS COMPLETELY EXPLAINED BY CHANGES IN THE SELECTION OF LIGHT INTENSITY AND SUBSTRATE TEMPERATURE. THE CHANGES IN SELECTION OF LIGHT INTENSITY AND SUBSTRATE TEMPERATURE WHICH OCCURRED IN THE SYMPATRIC REGION MUST BE EXPLAINED BY BEHAVIORAL ADJUSTMENTS OTHER THAN THOSE REFLECTED IN THE DAILY ACTIVITY PATTERN.

MACARTHUR AND LEVINS (1967) SHOWED THAT WHEN ECOLOGICAL SIMILARITY SURPASSES A MINIMAL LEVEL, INTERSPECIFIC SELECTIVE FORCES ACT TO PRODUCE COMPETITIVE NICHE DISPLACEMENT. WHILE THE RELATIVE NICHE POSITIONS OF I. RADIX AND I. SIRTALIS CHANGED IN THE SYMPATRIC REGION, THERE WAS NO NET DISPLACEMENT OF THE NICHE OCCUPIED (FIG. 5). THIS DOES NOT PRECLUDE A COMPETITIVE INTERACTION SINCE THERE WAS PROBABLY AN INCREASED SIMILARITY OF THE AVAILABLE NICHE. IT DOES, HOWEVER, DEMONSTRATE THAT COMPETITIVE INTERACTION, IF SIGNIFICANT AT ALL, WAS NOT LARGE. MEASUREMENT OF NICHE SEPARATION RELATIVE TO THE AVAILABLE NICHE BREADTH WAS NOT ATTEMPTED DUE TO THE DIFFICULTY OF QUANTIFYING AN AVAILABLE AS OPPOSED TO OCCUPIED NICHE.

THERMAL RELATIONS

THE HIGHER BODY TEMPERATURES OF I. RADIX IN THE ALLOPATRIC REGION (FIG. 7) SUGGEST THAT THIS SPECIES HAS A SLIGHTLY HIGHER PREFERRED TEMPERATURE THAN I. SIRTALIS. WHILE CLOACAL BODY TEMPERATURES OF I. SIRTALIS UPON CAPTURE WERE SLIGHTLY LOWER THAN THOSE REPORTED BY FITCH (1965) AS PREFERRED, BODY TEMPERATURES OF REPTILES CAPTURED IN THE FIELD ARE OFTEN FOUND TO BE LOWER THAN THOSE PREFERRED (LICHT ET AL., 1966) DUE, PERHAPS, TO GREATER CATCHABILITY AT SUB-OPTIMAL TEMPERATURES. IN SPITE OF THE ECOLOGICAL ADJUSTMENTS MADE BY BOTH SPECIES IN THE SYMPATRIC REGION, IN APPARENT COMPENSATION FOR MARGINAL AIR TEMPERATURES, BODY TEMPERATURES

BECAME MORE SIMILAR THERE. THIS WAS PRIMARILY DUE TO AN INCREASE IN THE BODY TEMPERATURE OF I. SIRTALIS WHICH INDICATES THAT I. SIRTALIS HAD PASSED ITS LIMIT OF BEHAVIORAL THERMAL ADJUSTMENT AND EXPLAINS WHY IT WAS UNABLE TO PENETRATE FURTHER INTO THE RANGE OF I. RADIX. BODY TEMPERATURES OF I. RADIX WERE NOT ALTERED APPRECIABLY IN THE SYMPATRIC REGION, AND IN FACT SHOWED A VERY SLIGHT INCREASE IN SPITE OF THE FACT THAT I. RADIX THERE WAS AT THE NORTHERN PERIPHERY OF ITS RANGE.

THAMNOPHIS RADIX, THEREFORE, HAD NOT PASSED ITS LIMIT OF BEHAVIORAL THERMAL ADJUSTMENT, BUT WAS PROBABLY AT OR VERY CLOSE TO THIS LIMIT IN THE SYMPATRIC REGION. NEITHER I. RADIX NOR I. SIRTALIS WOULD HAVE BEEN ABLE TO ALTER THEIR ACTIVITY PATTERNS MUCH FURTHER SINCE I. RADIX WAS ALREADY CONCENTRATING ITS ACTIVITY IN THE HOTTEST PART OF THE DAY AND I. SIRTALIS HAD VIRTUALLY ELIMINATED ITS MID-DAY ACTIVITY.

NEGATIVE SKEWNESS IN THE FREQUENCY DISTRIBUTIONS OF REPTILIAN BODY TEMPERATURES IS OFTEN REPORTED (COWLES AND BOGERT, 1944; BRATTSTROM, 1965). AS HEATH (1964) POINTS OUT, ALTHOUGH THIS PATTERN IS OFTEN INTERPRETED AS INDIRECT EVIDENCE FOR A PHOTOPHOBIC REACTION AT BODY TEMPERATURES HIGHER THAN THE MODAL ONE, SIMILAR PATTERNS ARE PRODUCED BY INANIMATE OBJECTS INCAPABLE OF MOVEMENT, AND NEED NOT BE ATTRIBUTED TO BEHAVIORAL THERMOREGULATION. THE SIGNIFICANCE OF THE PATTERN IN THE BODY TEMPERATURE DISTRIBUTIONS OF I. RADIX AND I. SIRTALIS IS, THEREFORE UNCERTAIN.

THE ORAL AND CLOACAL BODY TEMPERATURES OF I. RADIX AND I. SIRTALIS DEPENDED MOST STRONGLY UPON AIR TEMPERATURE (FIG. 8) AND NEXT MOST STRONGLY UPON SUBSTRATE TEMPERATURE. FLEHARTY (1967) RELATED CLOACAL TEMPERATURES OF I. ELEGANS, I. CYRTOPSIS AND I. RUFIPUNCTATUS PRIMARILY TO SUBSTRATE TEMPERATURE AND FOUND LITTLE EFFECT DUE TO AIR TEMPERATURE.

HOWEVER, FLEHARTY MEASURED AIR TEMPERATURE 24 CM ABOVE GROUND LEVEL RATHER THAN IMMEDIATELY ABOVE GROUND LEVEL AS IN THE PRESENT STUDY. HE MEASURED SUBSTRATE TEMPERATURE RIGHT AT GROUND LEVEL SO THAT IT REPRESENTED THE COMBINED EFFECTS OF AIR AND SUBSTRATE TEMPERATURE AS MEASURED IN THE PRESENT STUDY.

ORAL TEMPERATURES OF BOTH I. RADIX AND I. SIRTALIS DEPENDED STRONGLY UPON LIGHT INTENSITY. WHILE THE CLOACAL TEMPERATURES OF I. RADIX ALSO DEPENDED UPON THIS FACTOR, THOSE OF I. SIRTALIS DID NOT. THIS MAY BE EXPLAINED BY THE FACT THAT I. SIRTALIS WAS OFTEN CAPTURED ON THE SEDGE MAT OF A CLOSED MARSH, WITH ITS HEAD ABOVE THE MAT AND ITS TAIL BELOW, SHADED FROM THE SUN. LIGHT INTENSITY WAS NOT MEASURED UNDER THE SEDGE MAT.

ORAL AND CLOACAL TEMPERATURES OF I. SIRTALIS WERE INFLUENCED BY HABITAT. THE PROTECTION FROM THE SUN OFFERED THE SNAKE BY THE SEDGE MAT AND FOREST OF THE CLOSED MARSH HABITAT PROBABLY EXPLAINS THIS EFFECT.

THE DIRECT EFFECT OF SUBSTRATE MOISTURE UPON THE CLOACAL TEMPERATURES OF I. SIRTALIS, OTHER FACTORS BEING EQUAL, MAY HAVE BEEN DUE TO RELATIVE HUMIDITY NEAR THE SUBSTRATE, WHICH WAS NOT MEASURED. A DIRECT EFFECT OF RELATIVE HUMIDITY UPON BODY TEMPERATURES OF REPTILES, DUE TO INHIBITION OF EVAPORATIVE COOLING, WAS SUGGESTED BY COWLES AND BOGERT (1944). RELATIVE HUMIDITY WAS PROBABLY HIGH UNDER THE SEDGE MAT OF A CLOSED MARSH. SUCH AN EFFECT WOULD NOT BE EXPECTED TO BE COMPLETELY EXPLAINED BY THE HABITAT FACTOR SINCE THERE WAS CONSIDERABLE VARIABILITY IN THE MOISTURE OF A CLOSED MARSH, BOTH BETWEEN THE EDGES AND CENTRE OF THE MARSH AND THROUGHOUT THE SEASON AS THE MARSH BECAME DRY.

THE DIRECT EFFECT OF TIME OF CAPTURE, CODED AS A DEVIATION FROM MID-DAY, UPON THE CLOACAL TEMPERATURES OF I. SIRTALIS IS DIFFICULT TO

INTERPRET. DIEL VARIATIONS IN OTHER MEASURED ENVIRONMENTAL FACTORS SUCH AS LIGHT INTENSITY, AIR TEMPERATURE AND SUBSTRATE TEMPERATURE CANNOT, IN A MULTIPLE REGRESSION, EXPLAIN AN INDEPENDENT EFFECT DUE TO TIME OF CAPTURE. SUCH VARIATIONS WOULD, IN A SIMPLE REGRESSION, BE EXPECTED TO RESULT IN AN INVERSE RATHER THAN DIRECT RELATIONSHIP BETWEEN BODY TEMPERATURE AND TIME OF CAPTURE, WITH HIGHER BODY TEMPERATURES CLOSER TO MID-DAY. THE OBSERVED EFFECT OF TIME OF CAPTURE UPON THE CLOACAL TEMPERATURES OF I. SIRTALIS OVER AND ABOVE THOSE PRODUCED BY VARIATION IN OTHER MEASURED FACTORS SUGGESTS EITHER THE INFLUENCE OF UNMEASURED ENVIRONMENTAL FACTORS EXHIBITING A DIEL CYCLE OR AN INTRINSIC DIEL CYCLE IN CLOACAL TEMPERATURE.

THE OPPOSITE ECOLOGICAL ADJUSTMENTS MADE BY I. RADIX AND I. SIRTALIS TO THE SYMPATRIC ENVIRONMENT SUGGESTED THAT THE FORMER WAS COMPENSATING FOR A DECREASE IN AVAILABILITY OF HIGH AIR TEMPERATURES AND THE LATTER FOR AN INCREASE IN AVAILABILITY OF HIGH AIR TEMPERATURES. THIS IMPLIED THAT I. RADIX WAS BETTER ADAPTED TO HIGH SUMMER AIR TEMPERATURES THAN I. SIRTALIS. THE GREATER RATE OF ABSORPTION OF RADIANT ENERGY BY DEAD I. SIRTALIS THAN BY DEAD I. RADIX (FIG. 9) EXPLAINS THESE RESULTS. SINCE REMOVAL OF VARIABILITY IN WARMING RATES DUE TO VISUAL ALBEDO REDUCED THE DIFFERENCE BETWEEN THE WARMING RATES OF I. RADIX AND I. SIRTALIS, THE DIFFERENCE MAY BE ATTRIBUTED PARTLY TO THE HIGHER VISUAL ALBEDO OF I. RADIX (FIG. 10). HOWEVER, SINCE A LARGE DIFFERENCE BETWEEN THE WARMING RATES OF I. RADIX AND I. SIRTALIS REMAINED AFTER REMOVAL OF THE VISUAL ALBEDO EFFECT, OTHER FACTORS MUST CONTRIBUTE TO THE RATE DIFFERENCE. INFRA-RED RADIATION, WHICH WAS AN UNMEASURED VARIABLE IN THESE EXPERIMENTS MAY HAVE BEEN RESPONSIBLE FOR THE RESIDUAL DIFFERENCES IN WARMING RATE BETWEEN I. RADIX AND I. SIRTALIS, THE LATTER ABSORBING

INFRA-RED MORE EFFECTIVELY. BOTH VISIBLE AND INFRA-RED RADIATION ARE PROBABLY IMPORTANT TO THE THERMAL RELATIONS OF REPTILES. COLE (1943) HAS SHOWN THAT LIZARDS ARE ABLE TO ABSORB RADIANT ENERGY WELL FROM VISIBLE LIGHT AND THAT WARMING RATES UNDER VISIBLE LIGHT CORRELATE WELL WITH COLORATION. PORTER (1967) HAS SHOWN IN A VARIETY OF LIZARDS AND SNAKES THAT ENERGY ABSORPTION FROM THE VISIBLE SPECTRUM (400 - 700 MU) IS SLIGHTLY BETTER THAN THAT FROM THE NEAR INFRA-RED (700 - 1000 MU). HOWEVER, THE RELATIVE IMPORTANCE TO TEMPERATURE CONTROL IN THE SNAKE OF VISIBLE AS OPPOSED TO INFRA-RED LIGHT MUST ALSO DEPEND UPON THE RELATIVE PROPORTIONS OF THESE WAVELENGTHS REACHING THE SNAKE IN THE NATURAL ENVIRONMENT. THESE PROPORTIONS VARY WITH LATITUDE, SEASON AND WEATHER CONDITIONS. FROM DATA PRESENTED BY GATES (1966), IT WAS DETERMINED THAT AT SEA LEVEL ON A CLEAR DAY, BETWEEN 48% AND 50% OF THE TOTAL RADIANT ENERGY REACHING THE EARTH'S SURFACE AT THE LATITUDE OF THE STUDY AREA DURING THE SUMMER MONTHS FALLS WITHIN THE VISIBLE SPECTRUM. BETWEEN 27% AND 28% FALLS WITHIN THE NEAR INFRA-RED REGION OF THE SPECTRUM, WITH THE REMAINDER FALLING PRIMARILY IN THE FAR INFRA-RED. ON AN OVERCAST DAY THE PROPORTION OF FAR INFRA-RED WOULD BE EXPECTED TO BE INCREASED DUE TO THE GREENHOUSE EFFECT OF THE CLOUDS, AND VISIBLE LIGHT MIGHT BE OF LESS IMPORTANCE.

ALBEDO DIFFERENCES BETWEEN I. RADIX AND I. SIRTALIS CORRELATE WITH DIFFERENCES IN THERMAL TOLERANCE. THAMNOPHIS SIRTALIS IS REPORTED TO HAVE A SLIGHTLY LOWER CRITICAL TEMPERATURE THAN I. RADIX (FITCH, 1965). VINCENT (1971) FOUND I. SIRTALIS HIBERNATING AT BODY TEMPERATURES AS LOW AS -3° C WHILE BAILEY (1949) DID NOT FIND I. RADIX TO SURVIVE HIBERNATION AT TEMPERATURES LOWER THAN -2° C.

ACTIVITY

THE DEGREE OF BIMODALITY IN THE DAILY ACTIVITY PATTERN OF I. RADIX WAS FOUND BY HECKROTTE (1962) TO BE TEMPERATURE DEPENDENT. A SIMILAR TEMPERATURE DEPENDENCE IN THE DAILY ACTIVITY PATTERNS OF BOTH I. RADIX HAYDENI AND I. SIRTALIS PARIETALIS WAS SUGGESTED IN THE PRESENT STUDY BY THEIR DAILY ACTIVITY PROFILES UNDER CONTROLLED TEMPERATURE AND LIGHT REGIMES (FIGS. 12 AND 13). THIS TEMPERATURE DEPENDENCE EXPLAINS THE OPPOSITE ADJUSTMENTS IN ACTIVITY PATTERN MADE BY I. RADIX AND I. SIRTALIS TO THE SYMPATRIC ENVIRONMENT (FIG. 11) AND THE INCREASED IMPORTANCE OF TIME OF CAPTURE IN DISCRIMINATING BETWEEN THE NICHES OF I. RADIX AND I. SIRTALIS IN THIS REGION. BY BECOMING MOST ACTIVE NEAR MID-DAY, I. RADIX WAS ABLE TO SELECT HIGHER LIGHT INTENSITIES AND SUBSTRATE TEMPERATURES. BY AVOIDING THE HEAT OF MID-DAY, I. SIRTALIS WAS ABLE TO SELECT LOWER LIGHT INTENSITIES AND SUBSTRATE TEMPERATURES. JORDAN (1967), ON THE BASIS OF A SMALL SAMPLE OF SNAKES FROM ROADS WITHIN A REGION OF SYMPATRY IN MINNESOTA, SIMILARLY FOUND I. SIRTALIS TO BE ACTIVE EARLIER IN THE MORNING AND LATER IN THE EVENING THAN I. RADIX.

COMPETITIVE INTERACTION AND DENSITY-DEPENDENCE

THE PRIMARY IMPORTANCE OF PHYSICAL AS OPPOSED TO BIOTIC FACTORS IN THE ECOLOGY AND EVOLUTION OF TEMPERATE ZONE ANIMALS AND PLANTS HAS BEEN STRESSED BY DOBZHANSKY (1950) AND FISCHER (1961). BOGERT (1949) SUGGESTED THAT THIS WAS ESPECIALLY TRUE OF NORTHERN POIKILOTHERMS AND NOTED THAT STRINGENT THERMAL REQUIREMENTS MIGHT PREVENT SPECIALIZATION WITH RESPECT TO DENSITY-DEPENDENT ECOLOGICAL FACTORS. THE IMPORTANCE OF THERMAL FACTORS TO NORTHERN REPTILES HAS BEEN ILLUSTRATED BY GREGORY (1973) WHO ATTRIBUTED THE DISAPPEARANCE OF THE YOUNGEST YEAR CLASS AT A COMMUNAL DEN OF I. SIRTALIS TO REPRODUCTIVE FAILURE BROUGHT ON BY A COOL, CLOUDY SUMMER. IT IS ILLUSTRATED IN THE PRESENT STUDY BY THE FACT THAT ECOLOGICAL ADJUSTMENTS MADE BY BOTH I. RADIX AND I. SIRTALIS AT THEIR RANGE PERIPHERIES INVOLVED THOSE NICHE PARAMETERS MOST RELEVANT TO BODY TEMPERATURE CONTROL. MARKED REDUCTION IN THE RELATIVE FREQUENCY OF I. SIRTALIS CAPTURES FOLLOWING SPRING FLOODING OF MANY OF ITS DENS DURING THE PRESENT STUDY FURTHER EMPHASIZES THE SIGNIFICANCE OF CLIMATIC FACTORS IN REGULATING POPULATIONS OF NORTHERN REPTILES. THESE FACTORS ACT INDEPENDENTLY OF DENSITY AND OFTEN CATASTROPHICALLY. THE SIMILAR FEEDING HABITS OF I. RADIX AND I. SIRTALIS AND THE LACK OF EVIDENCE FOR NICHE DISPLACEMENT BETWEEN THEM SUGGEST THAT DENSITY-DEPENDENT FACTORS SUCH AS COMPETITIVE INTERACTION ARE PROBABLY NOT IMPORTANT AT NORTHERN LATITUDES. PIANKA (1974) POINTS OUT THAT THE LIMITING SIMILARITY REQUIRED TO PRODUCE COMPETITIVE NICHE DISPLACEMENT DEPENDS

UPON THE DEMAND/SUPPLY RATIO OF RESOURCES. IN GENERAL, NORTHERN
POIKILOTHERMS ARE PROBABLY FAR TOO VULNERABLE TO CLIMATIC FLUCTUATIONS
TO ACHIEVE POPULATION SIZES AND DEMAND/SUPPLY RATIOS SUFFICIENTLY
LARGE THAT DENSITY-DEPENDENT FACTORS CAN BECOME SIGNIFICANT.

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APPENDIX A. STATISTICS FOR ENVIRONMENTAL FACTORS BEFORE ADJUSTMENT
FOR SEASONAL TRENDS

| ALLOPATRIC | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME |
|--------------------|---------|----------|--------|-----------|------------|-------|
| <u>I. RADIX</u> | | | | | | |
| MEAN (R) | 1.419 | 1.324 | 12.665 | 24.555 | 21.379 | 1.781 |
| MEDIAN | 1.000 | 1.000 | 13.000 | 25.000 | 21.700 | 2.500 |
| VARIANCE | 0.323 | 0.471 | 2.425 | 13.575 | 9.760 | 1.423 |
| n | 105 | 105 | 105 | 105 | 105 | 105 |
| <u>I. SIRTALIS</u> | | | | | | |
| MEAN (S) | 2.641 | 1.880 | 12.506 | 22.054 | 19.024 | 2.044 |
| MEDIAN | 3.000 | 2.000 | 12.500 | 21.250 | 19.050 | 3.500 |
| VARIANCE | 0.320 | 0.832 | 2.453 | 11.954 | 14.353 | 2.460 |
| n | 92 | 92 | 92 | 92 | 92 | 92 |
| Z(R-S) | 15.103* | 4.785* | 0.710 | 4.912* | 4.720* | 1.308 |
| SYMPATRIC | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME |
| <u>I. RADIX</u> | | | | | | |
| MEAN (R) | 2.114 | 1.448 | 12.912 | 24.862 | 20.866 | 2.154 |
| MEDIAN | 2.000 | 1.000 | 13.400 | 24.600 | 20.600 | 2.500 |
| VARIANCE | 0.237 | 0.450 | 2.698 | 15.322 | 11.148 | 1.861 |
| n | 105 | 105 | 105 | 105 | 105 | 105 |
| <u>I. SIRTALIS</u> | | | | | | |
| MEAN (S) | 2.485 | 1.632 | 11.937 | 24.040 | 19.263 | 2.783 |
| MEDIAN | 2.000 | 1.000 | 12.000 | 24.000 | 19.500 | 3.500 |
| VARIANCE | 0.254 | 0.564 | 2.819 | 12.905 | 10.261 | 3.287 |
| n | 68 | 68 | 68 | 68 | 68 | 68 |
| Z(R-S) | 4.794* | 1.617 | 3.765* | 2.449 | 3.161* | 2.446 |

* Z SIGNIFICANT (P < .01)

APPENDIX B. REGRESSION STATISTICS FOR SEASONAL TRENDS OF ENVIRONMENTAL FACTORS IN THE ALLOPATRIC REGION ($Y = A + (B \times \text{DAY}) + (C \times \text{DAY}^2)$)

| Y: | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME |
|------------------------------------|---------|----------|--------|-----------|------------|--------|
| <u>T. RADIX (R)</u> | | | | | | |
| A | 1.704 | 1.810 | 14.987 | 20.049 | 14.707 | 2.730 |
| B _R | -0.032 | -0.100 | -0.685 | 1.458 | 2.322 | -0.548 |
| Z(B _R) | 0.353 | 0.915 | 2.914* | 2.526 | 5.230* | 3.055* |
| C _R | -0.003 | 0.002 | 0.042 | -0.101 | -0.174 | 0.058 |
| Z(C _R) | 0.355 | 0.207 | 1.976 | 1.942 | 4.365* | 3.603* |
| <u>T. SIRTALIS (S)</u> | | | | | | |
| A | 2.564 | 2.346 | 13.961 | 20.913 | 15.597 | 1.051 |
| B _S | -0.294 | -0.321 | -0.361 | 0.628 | 3.026 | -0.078 |
| Z(B _S) | 4.675* | 3.128* | 2.140 | 1.489 | 8.856* | 0.402 |
| C _S | 0.025 | 0.020 | 0.010 | -0.062 | -0.266 | 0.012 |
| Z(C _S) | 4.417* | 2.145* | 0.662 | 1.619 | 8.640* | 0.692 |
| <u>COMPARISON</u> | | | | | | |
| Z(B _R -B _S) | 2.382 | 1.480 | 1.121 | 1.161 | 1.257 | 1.787 |
| Z(C _R -C _S) | 2.824* | 1.325 | 1.216 | 0.607 | 1.834 | 1.940 |
| <u>POOLED</u> | | | | | | |
| A | 2.524 | 2.383 | 14.353 | 21.089 | 13.746 | 2.196 |
| B | -0.199 | -0.241 | -0.478 | 0.929 | 2.772 | -0.248 |
| Z(B) | 3.724* | 3.269* | 3.460* | 2.692* | 10.144* | 1.878 |
| C | 0.015 | 0.013 | 0.022 | -0.075 | -0.232 | 0.029 |
| (C) | 3.066* | 2.028 | 1.740 | 2.401 | 9.423* | 2.429 |

* Z SIGNIFICANT (P < .01)

APPENDIX C. REGRESSION STATISTICS FOR SEASONAL TRENDS OF ENVIRONMENTAL FACTORS IN THE SYMPATRIC REGION ($Y = A + (B \times \text{DAY}) + (C \times \text{DAY}^2)$)

| | Y: | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME |
|-------------------------------|------------------------------------|---------|----------|--------|-----------|------------|--------|
| <u>I. RADIX (R)</u> | | | | | | | |
| | A | 2.060 | 1.121 | 14.554 | 21.546 | 16.266 | 2.043 |
| | B _R | -0.031 | 0.257 | -0.490 | 1.705 | 2.122 | -0.155 |
| | Z(B _R) | 0.359 | 1.924 | 1.710 | 2.641* | 4.013* | 0.488 |
| | C _R | 0.007 | -0.031 | 0.025 | -0.168 | -0.193 | 0.029 |
| | Z(C _R) | 0.733 | -2.126 | 0.778 | 2.362 | 3.310* | 0.841 |
| <u>I. SIRTALIS (S)</u> | | | | | | | |
| | A | 2.443 | 2.164 | 13.557 | 22.549 | 15.166 | 1.738 |
| | B _S | -0.014 | -0.194 | -0.484 | 1.033 | 1.976 | 0.149 |
| | Z(B _S) | 1.201 | 1.450 | 1.691 | 1.600 | 3.736* | 0.470 |
| | C _S | 0.018 | 0.015 | 0.027 | -0.120 | -0.190 | 0.009 |
| | Z(C _S) | 1.891 | 0.993 | 0.869 | 1.682 | 3.263* | 0.246 |
| <u>COMPARISON</u> | | | | | | | |
| | Z(B _R -B _S) | 0.654 | 2.712 | 0.015 | 0.790 | 0.211 | 0.816 |
| | Z(C _R -C _S) | 0.927 | 2.576 | 0.073 | 0.533 | 0.037 | 0.518 |
| <u>POOLED</u> | | | | | | | |
| | A | 2.206 | 1.559 | 14.146 | 22.051 | 15.914 | 1.877 |
| | B | -0.052 | 0.078 | -0.480 | 1.393 | 2.038 | -0.012 |
| | Z(B) | 1.022 | 1.019 | 2.930* | 3.535* | 6.418* | 0.072 |
| | C | -0.010 | -0.014 | 0.025 | -0.144 | -0.189 | 0.019 |
| | Z(C) | 1.921 | 1.743 | 1.446 | 3.504* | 5.684* | 1.122 |

* Z SIGNIFICANT (P < .01)

APPENDIX D. STATISTICS FOR DISCRIMINANT SCORES AND ENVIRONMENTAL FACTORS AFTER ADJUSTMENT FOR SEASONAL TRENDS.

| ALLOPATRIC | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME | SCORE |
|--------------------|---------|----------|--------|--------------|---------------|-------|---------|
| I. RADIX | | | | | | | |
| MEAN (R) | 1.462 | 1.386 | 12.799 | 24.367 | 20.839 | 1.792 | -24.392 |
| MEDIAN | 1.131 | 1.247 | 12.991 | 24.704 | 20.616 | 1.835 | -30.445 |
| VARIANCE | 0.318 | 0.447 | 2.070 | 12.731 | 7.627 | 1.233 | 274.171 |
| n | 105 | 105 | 105 | 105 | 105 | 105 | 105 |
| I. SIRTALIS | | | | | | | |
| MEAN (S) | 2.592 | 1.810 | 12.353 | 22.269 | 19.639 | 2.009 | -62.808 |
| MEDIAN | 2.789 | 1.580 | 12.487 | 22.025 | 19.304 | 1.498 | -51.199 |
| VARIANCE | 0.269 | 0.691 | 1.866 | 11.865 | 7.842 | 2.449 | 290.631 |
| n | 92 | 92 | 92 | 92 | 92 | 92 | 92 |
| Z _(R-S) | 14.649* | 3.908* | 2.230 | 4.196* | 3.020* | 1.109 | 15.957* |
| SYMPATRIC | | | | | | | |
| I. RADIX | | | | | | | |
| MEAN (R) | 2.097 | 1.442 | 12.880 | 24.877 | 20.913 | 2.172 | 16.205 |
| MEDIAN | 1.979 | 1.158 | 13.170 | 25.081 | 20.848 | 2.218 | 15.475 |
| VARIANCE | 0.455 | 0.462 | 2.261 | 14.094 | 9.014 | 1.744 | 26.239 |
| n | 105 | 105 | 105 | 105 | 105 | 105 | 105 |
| I. SIRTALIS | | | | | | | |
| MEAN (S) | 2.513 | 1.641 | 11.987 | 24.016 | 19.190 | 2.735 | 10.855 |
| MEDIAN | 2.366 | 1.256 | 11.852 | 23.769 | 19.170 | 2.519 | 10.720 |
| VARIANCE | 0.481 | 0.564 | 2.437 | 12.513 | 8.334 | 3.022 | 28.671 |
| n | 68 | 68 | 68 | 68 | 68 | 68 | 68 |
| Z _(R-S) | 3.894* | 1.762 | 3.728* | 1.527 | 3.772* | 2.281 | 6.533* |

Z SIGNIFICANT (P < .01)

APPENDIX E. REGRESSION STATISTICS FOR DEPENDENCE OF ORAL AND CLOACAL TEMPERATURE ON ENVIRONMENTAL FACTORS (Y = I + (H X HABITAT) + (M X MOISTURE) + (L X LIGHT) + (A X AIR TEMP.) + (S X SUB. TEMP.) + (T X TIME))

| | I. RADIX (R) | | I. SIRTALIS (S) | | Y: | COMPARISON | |
|------|--------------|---------|-----------------|---------|------------------------------------|------------|---------|
| | ORAL | CLOACAL | ORAL | CLOACAL | | ORAL | CLOACAL |
| I | 6.941 | -1.620 | 4.420 | -0.113 | Z(I _R -I _S) | 0.780 | 2.492 |
| H | 0.259 | 0.222 | -1.081 | -1.090 | | | |
| Z(H) | 1.019 | 0.955 | 2.996* | 3.040* | Z(H _R -H _S) | 3.036* | 3.071* |
| M | -0.485 | -0.525 | 1.460 | 3.048 | | | |
| Z(M) | 2.130 | 2.523 | 1.838 | 3.864* | Z(M _R -M _S) | 2.355 | 4.380* |
| L | 0.626 | 0.358 | 0.448 | 0.073 | | | |
| Z(L) | 5.914* | 3.707* | 3.809* | 0.621 | Z(L _R -L _S) | 1.126 | 1.885 |
| A | 0.448 | 0.513 | 0.536 | 0.635 | | | |
| Z(A) | 9.216* | 11.550* | 9.746* | 11.607* | Z(A _R -A _S) | 1.196 | 1.721 |
| S | 0.165 | 0.164 | 0.273 | 0.382 | | | |
| Z(S) | 2.960* | 3.224* | 6.155* | 8.655* | Z(S _R -S _S) | 1.517 | 3.226* |
| T | -0.239 | -0.210 | 0.029 | 0.333 | | | |
| Z(T) | 1.886 | 1.817 | 0.205 | 3.378* | Z(T _R -T _S) | 1.611 | 3.574* |
| n | 201 | 201 | 155 | 155 | | | |

* Z SIGNIFICANT (P < .01)

APPENDIX F. CORRELATIONS BETWEEN ENVIRONMENTAL FACTORS MEASURED AT CAPTURE SITES (CORRELATION COEFFICIENTS BELOW THE DIAGONAL; Z VALUES ABOVE THE DIAGONAL)

| <u>201 T. RADIX</u> | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME |
|---------------------|---------|----------|--------|-----------|------------|--------|
| HABITAT | | 2.583* | 2.565 | 0.561 | 2.435 | 0.737 |
| MOISTURE | 0.180 | | 0.025 | 2.207 | 2.794* | 2.361 |
| LIGHT | 0.179 | 0.002 | | 4.557* | 2.251 | 1.275 |
| AIR TEMP. | 0.040 | -0.155 | 0.307 | | 6.610* | 2.920* |
| SUB. TEMP. | -0.170 | -0.194 | -0.158 | 0.424 | | 2.035 |
| TIME | 0.052 | -0.165 | -0.090 | -0.203 | -0.143 | |

| <u>155 T. SIRTALIS</u> | HABITAT | MOISTURE | LIGHT | AIR TEMP. | SUB. TEMP. | TIME |
|------------------------|---------|----------|---------|-----------|------------|---------|
| HABITAT | | 15.545* | 2.109 | 0.180 | 5.097* | 1.344 |
| MOISTURE | 0.783 | | 13.332* | 3.524* | 34.416* | 13.835* |
| LIGHT | 0.168 | 0.726 | | 2.357 | 0.901 | 5.162* |
| AIR TEMP. | -0.014 | -0.269 | 0.183 | | 3.510* | 1.977 |
| SUB. TEMP. | -0.374 | -0.938 | -0.071 | 0.268 | | 0.137 |
| TIME | -0.106 | -0.738 | -0.378 | -0.155 | 0.011 | |

* Z SIGNIFICANT (P < .01)

APPENDIX G. Box's TEST FOR MULTIVARIATE HOMOGENEITY OF VARIANCE
 APPLIED TO ENVIRONMENTAL DATA

| DATA | VARIANCE-COVARIANCE DETERMINANT | | | | | | |
|------------|---------------------------------|-------------------|---------|----------------|----------------|--------|--------|
| | <u>I.RADIX</u> | <u>I.SIRTALIS</u> | POOLED | A ₁ | A ₂ | M | F |
| UNADJUSTED | | | | | | | |
| ALLOPATRIC | 26.2967 | 135.7395 | 73.3695 | 0.02193 | 0.00107 | 50.725 | 2.361* |
| SYMPATRIC | 54.9118 | 58.2309 | 65.3793 | 0.02722 | 0.00165 | 25.904 | 1.199 |
| ADJUSTED | | | | | | | |
| ALLOPATRIC | 13.7526 | 53.4266 | 32.8000 | 0.03349 | 0.00130 | 45.237 | 2.082* |
| SYMPATRIC | 30.0906 | 36.6361 | 37.9683 | 0.040686 | 0.00198 | 26.041 | 1.189 |

* F SIGNIFICANT (P < .01)

APPENDIX H. BARTTLET'S TEST FOR HOMOGENEITY OF VARIANCE IN WARMING RATES.

| TWO-WAY | | | | | TWO-WAY | | | | |
|--------------------------|-------|----|-----------------|--------------------|----------------------------|-------|----|-----------------|--------------------|
| | SSDEV | df | si ² | ln si ² | | SSDEV | df | si ² | ln si ² |
| T. RADIX (R) | 12.71 | 37 | .3435 | -1.0685 | T. RADIX (R) | 12.22 | 36 | .3394 | -1.0804 |
| T. SIRTALIS (S) | 21.50 | 37 | .5811 | -0.5429 | T. SIRTALIS (S) | 20.07 | 36 | .5575 | -0.5843 |
| | | | | -1.6114 | | | | | -1.6647 |
| | | 74 | .4623 | -0.7715 | | | 72 | .4485 | -0.8019 |
| STEP 1. $\chi_1 = 2.432$ | | | | | STEP 2. $\chi_1 = 2.104$ | | | | |
| TWO-WAY | | | | | TWO-WAY | | | | |
| | SSDEV | df | si ² | ln si ² | | SSDEV | df | si ² | ln si ² |
| ALIVE (A) | 23.65 | 37 | .6392 | -0.4476 | ALIVE (A) | 23.05 | 36 | .6403 | -0.4459 |
| DEAD (D) | 10.70 | 37 | .2892 | -1.2407 | DEAD (D) | 9.30 | 36 | .2583 | -1.3535 |
| | | | | -1.6883 | | | | | -1.7994 |
| | | 74 | .4642 | -0.7675 | | | 72 | .4493 | -0.8001 |
| STEP 1. $\chi_1 = 5.451$ | | | | | STEP 2. $\chi_1 = 6.887^*$ | | | | |
| TWO-WAY | | | | | TWO-WAY | | | | |
| | SSDEV | df | si ² | ln si ² | | SSDEV | df | si ² | ln si ² |
| RA + SD | 14.90 | 37 | .4027 | -0.9096 | RA + SD | 14.02 | 36 | .3894 | -0.9430 |
| RD + SA | 19.37 | 37 | .5235 | -0.6472 | RD + SA | 18.78 | 36 | .5217 | -0.6507 |
| | | | | -1.5568 | | | | | -1.5937 |
| | | 74 | .4631 | -0.7698 | | | 72 | .4556 | -0.7862 |
| STEP 1. $\chi_1 = 0.612$ | | | | | STEP 2. $\chi_1 = 0.734$ | | | | |
| ONE-WAY | | | | | ONE-WAY | | | | |
| | SSDEV | df | si ² | ln si ² | | SSDEV | df | si ² | ln si ² |
| T. RADIX (RD) | 2.01 | 18 | .1117 | -2.1922 | T. RADIX (RD) | 1.71 | 17 | .1006 | -2.2967 |
| T. SIRTALIS (SD) | 6.39 | 18 | .3550 | -1.0356 | T. SIRTALIS (SD) | 5.52 | 17 | .3247 | -1.1248 |
| | | | | -3.2278 | | | | | -3.4215 |
| | | 36 | .2333 | -1.4553 | | | 34 | .2126 | -1.5481 |
| STEP 1. $\chi_1 = 5.271$ | | | | | STEP 2. $\chi_1 = 5.081$ | | | | |

* χ SIGNIFICANT (P < .01)

APPENDIX I. TEST FOR HOMOGENEITY OF REGRESSION OF WARMING RATES ON COVARIATES

| <u>TWO-WAY</u> | | | | <u>F STEP 1.</u> | <u>SSREG SSDEV df F STEP 2.</u> | | | |
|-------------------------|-------|-------|----|------------------|---------------------------------|-------|----|------|
| <u>T. RADIX (R)</u> | 27.19 | 12.71 | 37 | | 27.68 | 12.22 | 36 | |
| <u>T. SIRTALIS (S)</u> | 47.70 | 21.50 | 37 | | 49.13 | 20.07 | 36 | |
| | | 34.21 | 74 | | | 32.29 | 72 | |
| POOLED | 73.45 | 35.65 | 75 | | 75.23 | 33.87 | 74 | |
| | | 1.44 | 1 | 3.11 | | 1.58 | 2 | 1.76 |
| <u>TWO-WAY</u> | | | | <u>F STEP 1.</u> | <u>SSREG SSDEV df F STEP 2.</u> | | | |
| ALIVE (A) | 43.00 | 23.65 | 37 | | 43.60 | 23.05 | 36 | |
| DEAD (D) | 31.75 | 10.70 | 37 | | 33.15 | 9.30 | 36 | |
| | | 34.35 | 74 | | | 32.45 | 72 | |
| POOLED | 73.45 | 35.65 | 75 | | 75.23 | 33.87 | 74 | |
| | | 1.30 | 1 | 2.80 | | 1.47 | 2 | 1.58 |
| <u>TWO-WAY</u> | | | | <u>F STEP 1.</u> | <u>SSREG SSDEV df</u> | | | |
| RA + SD | 43.50 | 14.90 | 37 | | 44.18 | 14.02 | 36 | |
| RD + SA | 31.33 | 19.37 | 37 | | 31.92 | 18.78 | 36 | |
| | | 34.27 | 74 | | | 32.80 | 72 | |
| POOLED | 73.45 | 35.65 | 75 | | 75.23 | 33.87 | 74 | |
| | | 1.38 | 1 | 2.98 | | 1.07 | 2 | 1.17 |
| <u>ONE-WAY</u> | | | | <u>F STEP 1.</u> | <u>SSREG SSDEV df F STEP 2.</u> | | | |
| <u>T. RADIX (RD)</u> | 9.92 | 2.01 | 18 | | 10.25 | 1.71 | 17 | |
| <u>T. SIRTALIS (SD)</u> | 24.17 | 6.39 | 18 | | 24.95 | 5.52 | 17 | |
| | | 8.40 | 36 | | | 7.23 | 34 | |
| POOLED | 31.87 | 10.59 | 37 | | 33.17 | 9.29 | 36 | |
| | | 2.20 | 1 | 7.67* | | 2.06 | 2 | 4.00 |

* F SIGNIFICANT (P < .01)