To the Graduate Council:

I am submitting herewith a dissertation written by Matthew Kramer entitled "The Behavior and Natural History of the Florida Red-bellied Turtle, *Pseudemys nelsoni*: An Ethological Study." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology and a minor in Statistics.

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and Dean of the Graduate School

THE BEHAVIOR AND NATURAL HISTORY OF THE FLORIDA RED-BELLIED TURTLE, *PSEUDEMYS NELSONI*: AN ETHOLOGICAL STUDY

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Matthew Kramer

August 1989

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This dissertation is dedicated to Catherine, Bernard, Miriam and Jesse;

my family.

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ABSTRACT

Field work was conducted in 1983-1986 to gather data on social behavior of the Florida red-bellied turtle, *Pseudemys nelsoni*, by direct, underwater observation (Rock Springs run, Apopka, Florida) and home range analysis using mark-recapture and telemetry techniques (Rock Springs run and Payne's Prairie, Gainesville, Florida). Laboratory observations and experiments were conducted at the University of Tennessee in 1982-1986. A behavior catalog of *P. nelsoni* was constructed. While not comprehensive, it indicates that the social behavior of this species is complex and adapted for conditions of poor visibility. Conspecific identification probably occurs prior to courtship and other social interactions. Aggressive behavior, mostly by melanistic males, was directed toward conspecifics of both sexes. Aggressive behavior directed towards other males consisted largely of threats while females were bit and tugged on. Basking phases were not clearly discernable in *P. nelsoni* although some postures and behaviors were associated with the length of time an animal had spent basking. An investigation of how juvenile turtles assembled behavior revealed that alternating pairs of behaviors were the most common pattern. Variability in the patterning of behavior among observation periods and individual variation likely obscures much of the organization of their behavior. The most valuable techniques for investigating behavior patterns in this study were 1) identifying "units" of behavior, 2) first order transition matrices, 3) information theory, and 4) auto- and cross-associations. Precocial courtship was a frequent social event of juveniles in the laboratory. While this behavior's function is not obvious, many of its attributes coincide with those given for play behavior suggesting that the function of juvenile courtship is similar to one or more of the possible functions of play. The results of two laboratory experiments, one using positive reinforcement and the second punishment, suggest that these animals can

distinguish between a pair of turtles matched for size and pattern. To describe home range size and usage, the data were recast as a constrained nonlinear optimization problem and solved using a FORTRAN program. Home ranges were small at both the Apopka and Gainesville populations despite substantial habitat differences and the different techniques used to locate turtles. The entire home range could be traversed by an individual in one or two hours.

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PART 1

GENERAL INTRODUCTION AND OVERVIEW

CHAPTER 1

LITERATURE REVIEW

Semi-aquatic chrysemid turtles (*sensu* McDowell, 1964, comprising the genera *Chrysemys*, *Trachemys* and *Pseudemys*; hereafter, chrysemid) are traditional subjects in many areas of research, but basic behavioral studies are scant. This has impaired the advancement of other disciplines that would profit from a knowledge of these turtles' natural behavior. Psychologists have exploited the willingness of turtles to accept food in learning studies (reviewed in Burghardt, 1977). Physiologists rely on the resiliency of turtle preparations for research on vision, cardiac and anaerobic metabolism (e.g., Gatten, 1974; Neumeyer and Jaeger, 1985). The relatively recent discovery of temperature-dependent sex determination in some emydid (Emydidae) turtles (Vogt and Bull, 1982) has secured this group's popularity for laboratory investigations.

Ethologically oriented lab research on these turtles has primarily been concerned with courtship. One of the earliest descriptions of courtship was by Taylor (1933) on *Trachemys scripta elegans* and *Chrysemys picta*. Subsequent observations of these genera were conducted by Ernst (1971), on *C. picta*; Davis and Jackson (1970, 1973) and Jackson and Davis (1972*a*) on *T. scripta*; Marchand (1944) and Jackson and Davis (1972*b*) on *P. concinna suwanniensis*; and Jackson (1977) on *P. nelsoni*. Cagle (1955) was the first to note that captive juvenile turtles occasionally vibrated the nails of their forefeet near novel turtles or objects.

There has been considerably more interest in turtle natural history. Homing and orientation in chrysemid turtles have been investigated by a number of authors (e.g., Anderson, 1958; Bennet et al., 1970; Cagle, 1944; DeRosa and Taylor, 1982; Emlen,

1969; Ernst, 1970; Gibbons and Smith, 1968; Murphy, 1970; Ortleb and Sexton, 1964; Williams, 1952). Most of the species in this group appear capable of orientation and homing if displaced less than a mile from the capture site. If released on land the most important sensory modality is vision (identification of landmarks). When released in the same stretch of water olfaction may be equally or more important.

Although feeding ecology has been researched by several authors (Clark and Gibbons, 1969; Hart, 1983; Knight and Gibbons, 1968; Parmenter, 1980; Raney and Lachner, 1942), food preference in chrysemid turtles has been studied only by Mahmoud and Lavenda (1969). They showed that food preferences of juvenile *Trachemys scripta* were transitory. Using a different design and *Chelydra* (Chelydridae), Burghardt and Hess (1966) found that food preferences established during the first feeding episodes appear more permanent.

Circadian rhythms have been demonstrated in the diurnal species, *Chrysemys picta* (Graham, 1972) and *Trachemys scripta* (Cloudsley-Thompson, 1982). The activity patterns are influenced by temperature and are possibly entrained by ultraviolet radiation, at least in *T. scripta* (Cloudsley- Thompson, 1982).

The remaining research on chrysemid turtles has dealt with terrestrial activity, nesting and basking. There are no quantified descriptions of nesting but all studies agree that the nest hole is dug in an extremely stereotyped fashion with the hind legs alone (Allen, 1938; Cagle, 1937; Mahmoud, 1969). Basking has been more thoroughly studied and a partial ethogram of the basking behavior of *Trachemys scripta* has been prepared by Auth (1975). Other relevant studies include Boyer (1965), Hennemann (1979), Litwin (1976), Lovich (1984), Riedesel, et al. (1971), and Zipko (1982).

CHAPTER 2

RATIONALE: WHY STUDY TURTLES?

To interpret an animal's behavior in the lab correctly, one must also study it in the field. Only in the field does the relevance of many learning paradigms become clear (e.g., illness induced avoidance in the rat, summarized in Garcia et al., 1973). Similarly, irrelevant behavior patterns in artificial situations may be put into perspective by understanding their use in the wild (e.g., raccoons "washing" coins, Breland and Breland, 1961).

Unfortunately, laboratory projects often evolve with little regard for field work. For example, wild rats were not studied in the field until the late 1950's (Barnett, 1975) although domestic and occasional wild rats were widely used as experimental subjects during the preceding 30 years.

A similar situation exists with chrysemid turtles. As mentioned above, only basking behavior has been systematically investigated in the field. Basking has little relevance to the kinds of questions asked by comparative psychologists. However, an understanding of aquatic behavior of the animals in the field may do much to help interpret and complement lab work, as well as suggest future lab work.

There are many reasons for studying turtle behavior in its own right. Turtles are probably the most primitive of the extant reptiles, already separate from other lineages by the early Permian (Prichard, 1979). They are moderately successful and show a wide variety of forms. Part of the reason for their success must lie with their behavior. Of special interest is the balance between remarkably stereotyped behaviors (e.g., nest hole digging) and behavioral flexibility. In a natural situation, Moll (1980) describes how a

turtle population adapted to a radically altered (polluted) environment through diet modification. When studying a conservative behavior pattern such as nesting, we are studying an old pattern indeed. Virtually all extant turtles dig nest holes in the same manner (Ehrenfeld, 1979) and presumably extinct ones did as well. This pattern may be over 250 million years old.

Turtles are the only extant reptile group with a protective shell. Carrying a shell has a great effect on mobility and locomotion (Walker, 1979). Their slowness has strongly influenced the manner in which they confront ecological pressures. Although predation on adults may be low, juvenile chrysemid turtles are vulnerable to aquatic predators because they swim slowly and lack the buoyancy control possessed by adults (unpubl. obs.). Thus, they must depend on crypsis and concealment to avoid predators during the first few years of their life. Rapid growth in chrysemid turtles is not possible due to the foraging inefficiency of a slow moving predator and the high calcium requirement of the shell for growth.

Due to their foraging inefficiency, one would expect young turtles to be opportunistic generalists, eating whatever and whenever they can. This is precisely why they make such good study animals in the laboratory. As they get older the percentage of plant matter in their diet increases. Adults of the largest species are almost completely herbivorous (Ernst and Barbour, 1972; Hart, 1983). The constraints forcing turtles to be food generalists may have aided them evolutionarily. Over the long run, a food specialist is more likely to become extinct.

CHAPTER 3

OBJECTIVES

This study had three major objectives: (1) to describe the overt behaviors of a semi-aquatic turtle in the field, (2) to analyze selected behaviors and behavior sequences in the laboratory or field and, if possible, to investigate problems made apparent during field observations, and (3) to estimate the number of conspecifics an individual regularly encounters.

As a first step in describing the behavior of *Pseudemys nelsoni* a catalog of the behaviors of this turtle was constructed (Part 2). Both Lorenz and Tinbergen have advocated the utility of ethograms (Schleidt et al., 1984) and Lehner (1979, p. 46) states that, "... it should be the starting point for any ethological research, especially species-oriented research." As in Byers and Bekoff's (1981) field study of peccaries, frequency and durations of the behaviors of *P. nelsoni* in the field were recorded, if possible, for subsequent use in analyzing social and maintenance behaviors.

Schleidt, et al. (1984), among others, point out that the social behavior of turtles has been only cursorily investigated (see above). Since most interactions seen in the field were dyadic, male-male, male-female, and female-female interactions are described. Ascribing functions to some of these behaviors is problematic, thus the most likely explanations are put forward with the goal of clarifying how future research may resolve these problems.

The second objective is divided into Parts 3-6. In Part 3, I examine sequences of behavior exhibited by juvenile *P. nelsoni* kept in the laboratory, and in Part 4 basking patterns of adults in the field. There are several related reasons for an attempt to analyze sequences of behavior. One is to group behaviors into categories that share common

causes or motivation (Slater, 1973). Sequence analysis is also useful to test for behavioral differences among individuals or between species (Crane, 1978). Finally, "rules" of behavior may be discovered that can aid in understanding an animal's behavior (Dawkins and Dawkins, 1974). The sequence analyses of laboratory juveniles were made primarily to uncover "rules" and individual differences in behavior. Basking behavior was analyzed to determine if the basking phases ("rules") proposed by Auth (1975) for *Trachemys scripta* might also describe basking patterns of *P. nelsoni.*

In Part 5, precocial courtship in juveniles is examined. Courtship behavior in this species has only recently been described (Kramer and Fritz, 1989). Courtship-like behavior was a frequent social event of juveniles maintained in the laboratory. Other researchers (Cagle, 1955; Petranka and Phillippi, 1978) have also noted precocial courtship in other species, although it was less frequent than seen in these juveniles. In this Part, precocial courtship is described and quantified. Preferences of individuals to "court" others is examined. As with some other social behaviors its function is not known. However, many of the attributes of this behavior coincide with those Fagen (1981) gives for play behavior suggesting that the function of juvenile courtship may be similar to one or more of the possible functions of play.

Individual recognition may play a prominent role in the organization of social animals, especially vertebrates (Barnard and Burk, 1979; Johnson, 1977). Chrysemid turtles are often found in dense populations (Bury, 1979), suggesting that they have been under selective pressure to evolve mechanisms to minimize agonistic confrontations. One such mechanism is the establishment and maintenance of a dominance hierarchy (Bernstein, 1981), presumably requiring individual recognition. In Part 6, I examine the evidence for individual recognition in turtles. Two experiments to test for individual recognition are described and the results compared with similar tests on other taxa.

If the social organization of these animals is mediated through individual recognition, one expects most individuals to regularly encounter a limited number of conspecifics. In these turtles, this could be accomplished if home range size was inversely proportional to population density so that the number of individuals encountered does not exceed the number that can be recognized. Thus, it was of interest to estimate the number of conspecifics an individual would regularly encounter (objective 3) by estimating home range size and population density. To estimate home range size and utilization, I adapted the mathematical technique developed by Ford and Krumme (1979), where the data are recast as a constrained nonlinear optimization problem, the solution yielding the desired estimates. Population estimates were made using standard techniques (Begon, 1979). The results are consistent with a social system based on individual recognition.

LITERATURE CITED

Allen, E.R. 1938. Notes on the feeding and egg-laying habits of the *Pseudemys*. Proc. Fla. Acad. Sci. 3, 105-108.

Anderson, P.K. 1958. The photic responses and water-approach behavior of hatchling turtles. Copeia 1958, 211-215.

Auth, D.L. 1975. Behavioral ecology of basking in the yellow- belled turtle, *Chrysemys scripta scripta* (Schoepff). Bull. Fla. State Museum Biol. Sci. 20, 1-45.

Barnard, C.J. and T. Burk. 1979. Dominance hierarchies and the evolution of "individual recognition". J. Theor. Biol. 81, 65-73.

Barnett, S.A. 1975. The rat: A study in behavior, 2nd ed. Univ. of Chicago Press.

Begon, M. 1979. Investigating animal abundance. Capture-recapture for biologists. Univ. Park Press, Baltimore. 97 pp.

Bennett, D.H., J.W. Gibbons and J.C. Franson. 1970. Terrestrial activity in aquatic turtles. Ecology 51, 738- 740.

Bernstein, I.S. 1981. Dominance: The baby and the bathwater. Beh. Brain Sci. 4, 419-457.

Boyer, D.R. 1965. Ecology of the basking habit in turtles. Ecology 46, 99-118.

Breland, K. and M. Breland. 1961. The misbehavior of organisms. Am. Psychol. 16, 681-684.

Burghardt, G.M. 1977. Learning processes in reptiles. *In* Gans, C. and D. Tinkle (Eds.). The Biology of the Reptilia, vol. 7. Academic Press, N.Y. Pp. 555-681.

Burghardt, G.M. and E.H. Hess. 1966. Food imprinting in the snapping turtle. Science 151, 108-109.

Bury, R.B. 1979. Population ecology of freshwater turtles. *In* Harless, M. and H. Morlock (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, N.Y. Pp. 571-602.

Byers, J.A. and M. Bekoff. 1981. Social, spacing and cooperative behavior of the collared peccary, *Tayassu tajacu*. J. Mammol. 62(4), 767-785.

Cagle, F.R. 1937. Egg laying habits of the slider turtle (*Pseudemys troostii*), the painted turtle (*Chrysemys picta*), and the musk turtle (*Sternotherus odoratus*). J. Tennessee Acad. Sci. 12, 87-95.

Cagle, F.R. 1944. Home range, homing behavior, and migration in turtles. Misc. Publ. Museum Zool. Univ. Mich. 61, 1-34.

Cagle, F.R. 1955. Courtship behavior in juvenile turtles. Copeia 1955, 307.

Clark, D.B. and J.W. Gibbons. 1969. Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. Copeia 1969, 704-706.

Cloudsley-Thompson, J.L. 1982. Rhythmic activity in young red- eared terrapins (*Pseudemys scripta elegans*). Brit. J. Herpetol. 6, 188-194.

Crane, V.R. 1978. On fitting low-order Markov chains to behaviour sequences. Anim. Behav. 26, 332-338.

Davis, J.D. and C.G. Jackson, Jr. 1970. Copulatory behavior in the red-eared turtle, *Pseudemys scripta elegans* (Wied). Herpetologica 26, 238-240.

Davis, J.D. and C.G. Jackson, Jr. 1973. Notes on the courtship of a captive male *Chrysemys scripta taylori*. Herpetologica 29, 62-64.

Dawkins, M. and R. Dawkins. 1974. Some descriptive and explanatory stochastic models of decision-making. *In* McFarland, D.J. (Ed.). Motivational control systems analysis. Academic Press, N.Y. Pp. 119-168.

DeRosa, C.T. and D.H. Taylor. 1982. A comparison of compass orientation mechanisms in three turtles (*Trionyx spinifer*, *Chrysemys picta* and *Terrapene carolina*). Copeia 1982, 394- 399.

Ehrenfeld, D.W. 1979. Behavior associated with nesting. *In* Harless, M. and H. Morlock (Eds.). Turtles: Perspectives and research. John Wiley and Sons, N.Y. Pp. 417-434.

Emlen, S.T. 1969. Homing ability and orientation in the painted turtle *Chrysemys picta marginata*. Behaviour 33, 58- 76.

Ernst, C.H. 1970. Homing ability in the painted turtle, *Chrysemys picta* (Schneider). Herpetologica 26, 399-403.

Ernst, C.H. 1971. Observations on the painted turtle, *Chrysemys picta*. J. Herpetol. 5, 216-220.

Ernst, C.H. and R.W. Barbour. 1972. Turtles of the United States. Univ. of Kentucky Press. 347 pp.

Fagen, R. 1981. Animal Play Behavior. Oxford University Press, Inc., N.Y. 684 pp.

Ford, R.G. and D.W. Krumme. 1979. The analysis of space use patterns. J. Theor. Biol. 76, 125-155.

Garcia, J., C. Clarke and W. Hankins. 1973. Natural responses to scheduled rewards. *In* Bateson, P.P.G. and P.H. Klopfer (Eds.). Perspectives in ethology, vol 1. Plenum Press, N.Y. Pp. 1-41.

Gatten, R.E., Jr. 1974. Effects of temperature and activity on aerobic and anaerobic heart rate in the turtles *Pseudemys scripta* and *Terrapene ornata*. Comp. Biochem. Physiol. 48A, 619-648.

Gibbons, J.W. and M.H. Smith. 1968. Evidence of orientation by turtles. Herpetologica 24, 331-333.

Graham, T.E. 1972. Temperature-photoperiod effects on diel locomotor activity and thermal selection in the turtles, *Chrysemys picta* (Schneider), *Clemmys guttata* (Schneider) and *Sternotherus odoratus* (Latreille). Ph.D. Dissertation, Univ. of Rhode Island. 179 pp.

Hart, D.R. 1983. Dietary and habitat shift with size of red- eared turtles (*Pseudemys scripta*) in a southern Louisiana population. Herpetologica 39, 285-290.

Hennemann, W.W. 1979. The influence of environmental cues and nutritional status on frequency of basking in juvenile Suwannee terrapins (*Chrysemys concinna*). Herpetologica 35, 129.

Jackson, C.G., Jr. 1977. Courtship observations on *Chrysemys nelsoni* (Reptilia, Testudines, Testudinidae). J. Herpetol. 11, 221-222.

Jackson, C.G., Jr. and J.D. Davis. 1972*a*. A quantitative study of the courtship display of the red-eared turtle, *Chrysemys scripta elegans* (Wied). Herpetologica 28, 58-64.

Jackson, C.G., Jr. and J.D. Davis. 1972*b*. Courtship display behavior of *Chrysemys concinna suwanniensis*. Copeia 1972, 385-387.

Johnson, V.R. 1977. Individual recognition in the banded shrimp *Stenopus hispidus* (Oliver). Ani. Behav. 25, 418-428.

Knight, A.W. and J.W. Gibbons. 1968. Food of the painted turtle, *Chrysemys picta*, in a polluted river. Amer. Midl. Natur. 80, 558-562.

Kramer, M. and U. Fritz. 1989 Courtship behavior of the turtle, *Pseudemys nelsoni*. J. Herpetol. 23, 84-86.

Lehner, P.N. 1979. Handbook of ethological methods. Garland STPM Press, N.Y. 403 pp.

Litwin, S.C. 1975. Basking activity in the eastern painted turtle, *Chrysemys picta picta*. Master's Thesis, Rutgers Univeristy. 54 pp.

Lovich, J.E. 1984. An analysis of aggressive basking behavior in the eastern painted turtle. Master's Thesis, George Mason University. 79 pp.

McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London 143, 239-279.

Mahmoud, I.Y. 1969. Nesting behavior in the western painted turtle, *Chrysemys picta bellii*. Herpetologica 24, 158-162.

Mahmoud, I.Y. and N. Lavenda. 1969. Establishment and eradication of food preferences in red-eared turtles. Copeia 1969, 298-300.

Marchand, L.J. 1944. Notes on the courtship of a Florida terrapin. Copeia 1944, 191-192.

Moll, D. 1980. Dirty river turtles. Natur. Hist. Mag. 89, 42- 49.

Murphy, G.G. 1970. Orientation of adult and hatchling red- eared turtles, *Pseudemys scripta elegans*. Ph.D. Dissertation, Mississippi State Univ. 93 pp.

Neumeyer, C. and J. Jager. 1985. Spectral sensitivity of the freshwater turtle, *Pseudemys scripta elegans*: Evidence for the filter effect of colored oil droplets. Vision Res. 25, 833-838.

Ortleb, E.P. and O.J. Sexton. 1964. Orientation of the painted turtle, *Chrysemys picta*. Am. Midl. Nat. 71, 320-334.

Parmenter, R.R. 1981. Digestive turnover rates in freshwater turtles: The influence of temperature and body size. Comp. Biochem. Physiol. 70A, 235-238.

Petranka, J.W. and A. Phillippi. 1978. Observations on the courtship behavior of juvenile *Chrysemys concinna concinna* and *Chrysemys floridana hoyi* (Reptilia, Testudines, Emydidae). J. Herpetol. 12(3), 417-419.

Prichard, P.C.H. 1979. Encyclopedia of turtles. T.F.H. Publications, Inc. Ltd. 895 pp.

Raney, E.C. and E.A. Lachner. 1942. Summer food of *Chrysemys picta* in Chautauqua Lake, New York. Copeia 1942, 83-85.

Riedesel, M.L., J.L. Cloudsley-Thompson and J.A. Cloudsley- Thompson. 1971. Evaporative thermoregulation in turtles. Physiol. Zool. 44, 28-32.

Schleidt, W.M., G. Yakalis, M. Donnelly and J. McGarry. 1984. A proposal for a standard ethogram, exemplified by an ethogram of the bluebreasted quail (*Coturnix chinensis*). Z. Tierpsychol. 64, 193-220.

Slater, P.J.B. 1973. Describing sequences of behavior. *In* Bateson, P.P.G. and P.H. Klopfer (Eds.). Perspectives in Ethology, Vol. I., Plenum Press, N.Y. Pp. 131-153.

Taylor, E.H. 1933. Observations on the courtship of turtles. Univ. of Kansas Science Bull. 21, 269-271.

Vogt, R.C. and J.J. Bull. 1975. Temperature controlled sex determination in turtles: Ecological and behavioral aspects. Herpetologica 38, 156-164.

Walker, W.F., Jr. 1979. Locomotion. *In* Harless, M. and H. Morlock (Eds.). Turtles: Perspectives and research. John Wiley and Sons, N.Y. Pp. 435-454.

Williams, J.E. 1952. Homing behavior of the painted turtle and musk turtle in a lake. Copeia 1952, 184-186.

Zipko, S.J. 1982. The basking behavior of painted turtles. Amer. Biol. Teacher 44, 406-412.

PART 2

THE MAINTENANCE AND SOCIAL BEHAVIORS OF *PSEUDEMYS NELSONI*

CHAPTER 1

INTRODUCTION

Carpenter and Ferguson's (1977) review of stereotyped social behavior in reptiles attests to herpetologists' interest in describing the behaviors of their study animals. The descriptions generally fall into two classes: (1) those constructed for making quantitative assessments of an animal's behavior (e.g., Jackson and Davis, 1972*a*), and (2) those noted due to their peculiarity (e.g., Cagle, 1955), despite the frequent unavailability of the animal's typical behavior in the literature. Systematic attempts to catalog all or most behaviors of any reptile species have been lab oriented (e.g., Greenberg, 1977). This is surprising because the best studied reptiles, lizards, are usually diurnal, have small home ranges, and are tolerant of observers (e.g., Rand, 1964, 1967; but see Sugarman and Hacker, 1980). For turtles, the average number of acts described per species in Carpenter and Ferguson (1977) is only 10.15 (Schleidt et al., 1984) with many species absent. I found no published complete ethogram of any turtle. Here I catalog the behaviors of *Pseudemys nelsoni*, the Florida red-bellied turtle, and present the contexts in which these behaviors are exhibited.

Pseudemys nelsoni (Testudines: Emydidae) is a member of a group that includes the genera *Trachemys* and *Chrysemys*. There are three (or four, according to Ward, 1984) closely related *Pseudemys* red-bellied turtles that, at one time, were probably distributed continuously along the gulf and eastern coast of the United States. *P. nelsoni* is the southernmost member of this group and presently occupies peninsular Florida (Ward, 1984). *P. floridana peninsularis*, also observed during this study, is the southernmost

subspecies of *P. floridana* (Ward, 1984). The natural history of both species is described by Ernst and Barbour (1972).

These three genera share a number of behavioral traits, such as frequent basking (Auth, 1975; Litwin, 1975; Zipko, 1982) and a complex and prolonged courtship (Jackson and Davis, 1972*a*, *b*; Kramer and Fritz, 1989; Marchand, 1944; Taylor, 1933; but see Davis and Jackson, 1973, for an exception). Social structure is poorly understood although agonistic interactions have been observed in several species (Bury et al., 1979; Kramer, 1986; Lardie, 1983; Rundquist, 1985). Both a territorial and hierarchical social structure have been suggested for *Trachemys scripta* (Lardie, 1983). A size-based hierarchy for access to preferred positions is likely on basking sites (Auth, 1976; Bury et al., 1979; Lovich, 1984). Individuals of these species generally share their home range with many other individuals (Bury, 1979; Kramer, 1986) suggesting a well developed social system.

Choice of Subject

Reasons for choosing *Pseudemys nelsoni*, rather than another emydid turtle for this study, include the following. (1) Populations of this species occur in clear spring runs, the best natural environment for conducting underwater observations on North American emydid turtles. Of the suitable spring runs that I visited, *Pseudemys nelsoni* populations were denser than those of *P. floridana* or *P. concinna*. (2) Individuals appeared to be more tolerant of an observer than *P. floridana*. *P. concinna*, in Rainbow run, Fla., were also tolerant of an observer but the number of these turtles has so greatly diminished since Marchand's (1945) study that animals there were difficult to find. Finally, (3) the animals are large and sexually dimorphic. The sexes were readily distinguishable underwater and

when basking because males have a lower shell profile, long front claws, large heavy tail, and are frequently melanistic. Due to confusion with *P. floridana*, it was occasionally difficult to ascertain the species identity of an individual without disturbing it.

Since *Pseudemys nelsoni* is not widely distributed and possesses no outstanding characteristics, few researchers have taken pains to study it (for a review of the literature see Jackson, 1978). Only three behavioral studies have been quantitative. In a preliminary report, I discussed the social interactions in *P. nelsoni* based largely on underwater observations (Kramer, 1986). Kramer and Fritz (1989) described courtship behavior based on laboratory and field data. Bjorndal (1986) examined the influence of conspecifics on feeding rates in the laboratory. Other behavioral reports on this turtle have been anecdotal. These include a brief description of courtship behavior by Lardie (1973) and a note by Jackson (1977) reporting a female titillating (courting) a male. Some basking behaviors have been noted by Prichard and Greenhood (1968) as well as a thermal tolerance above that of two sympatric species, *Pseudemys floridana* and *P. concinna*. Basking females were also observed by Auth (1975) although their behavior apparently did not differ enough from *Trachemys scripta* to warrant mention.

The Use of Ethograms

An ethogram is a complete catalog of an animal's behaviors (Lehner, 1979). Many studies present only a partial ethogram of one behavior category, e.g., comfort behavior (Ainley, 1974), while others are more complete (e.g., Greenberg, 1977; Phillips, 1977). However, if one's intent is to begin research on a poorly studied species, construction of an ethogram is a logical first step (Jennings, 1906 [in Schleidt et al., 1984]; Lehner, 1979). The primary value of an ethogram or catalog of behaviors is to present the behavioral

repertoire of a species. This answers, in part, how an animal behaves by providing a description of its behaviors.

Catalogs of behavior have additional, direct applications. Catalog construction uncovers inadequacies in the investigator's understanding of the species' behavior, often through comparison with other catalogs. This may encourage additional hours of observation, suggest novel contexts in which to study the organism, or prompt a detailed analysis of certain behaviors. A good ethogram may benefit researchers searching for a suitable species to investigate broad ethological questions. A large collection of ethograms on diverse taxa may be necessary to investigate phylogenetic and adaptive trends (e.g., Moynihan, 1970).

Emotional Behavior

The catalog of behaviors that I present below would not be complete without reference to the apparent emotional behavior displayed by turtles. There are several reasons to justify its inclusion. First, some behaviors looked like emotional responses because changes in body posture and muscle tone were similar to the emotional behavior described for more familiar animals (e.g., dogs, see Darwin, 1965) in similar situations. Second, ethologists working on vertebrates usually credit their subjects with emotions, often thought to motivate some behaviors (Hinde, 1985; Weinrich, 1980). The evolutionary continuity of emotion (Burghardt, 1985) has intuitive appeal and greatly aids informal descriptions of an animal's behavior. Third, some behaviors are highly correlated with particular emotional expressions (examples in Darwin, 1965). Fourth, classifying behaviors by shared emotional states, like classifying by context or function, may be useful in revealing the organization of behavior.

CHAPTER 2

MATERIALS AND METHODS

This catalog of behaviors is based on observations conducted at a field site in Apopka, Florida, supplemented with observations in Payne's Prairie, Florida, and the laboratory. In the field, observations on animals in the water were made by snorkeling, or from a canoe or bank. Basking animals were observed from a canoe or bank. In the lab, observations were made on animals in large aquaria or wading pools. Details follow.

Field Sites

The study area was located in the upper portion of Rock Springs run, Apopka, Orange County, Fla., located at 28°45'20"N, 81°29'58"W. It was two km downstream from Rock Springs and comprised a 980 m section of the river. The water remained relatively clear throughout the year and water temperature probably did not deviate from 21°C by more than 2°C. Predominant macrophytes along the banks were *Nuphar luteum, Pontederia lanceolata, Typha* spp., *Hydrocotyle umbellata*, and *Pistia stratiotes*. *Vallisneria americana* and *Hydrilla verticillata* were abundant in the middle of the run if the water was shallow and moving quickly. Elsewhere the substrate consisted of soft mud. *Oscillatoria* spp., a preferred food of these turtles, was found in clumps on the bottom and floating at the surface throughout the study area. Six field trips for observing animals were made from 1983-1985 (Table 1)†. Some behavioral data were collected at Payne's Prairie, Gainesville, Alachua County, Fla. during a brief telemetry study in 1986.

† Tables and figures are located in an appendix following the Literature Cited at the end of each Part.

Marking

Pseudemys nelsoni and *P. floridana* individuals were collected indiscriminately. One hundred and twenty nine *P. nelsoni* (73 male, 56 female) and 43 *P. floridana* (23 male and 20 female) were marked. They were captured by diving, placed in a canoe, and brought ashore for measuring and marking.

Three types of marks were given to all but the smallest turtles. These were 1) up to three permanent holes drilled in the first three or last eight marginals (Cagle, 1939), 2) a 1.3 cm (1/2 in) fabric fastener inserted through each hole, and 3) a number painted on the carapace in four places with a rubberized paint marker (Sport Divers Mfg. felt tip marker) or an epoxy paint. The number painted on the carapace was decipherable for 1-3 months. The fabric fasteners remained in the holes for about one year. The fasteners permitted individual identification after the paint had worn off and the holes obscured by algae.

Underwater Observations

Due to rapid chilling when motionless underwater, only two or three one-hour observation periods were possible per day despite using a wetsuit. Figure 1 gives the distribution of hours of observation by time of year and by time of day.

Animals were located by swimming upstream slowly along one of the banks. When an individual or group was seen their behaviors were noted by writing on roughened white Plexiglas sheets with a pencil. Some photographs were taken using a Nikonos II and Tri-X film push-processed to 1600 ASA. Occasionally I was able to follow animals that appeared undisturbed by my presence. More often, however, animals exhibited a startle/escape response (see below) when I approached closely unless they were engaged in

courtship or agonistic encounters. By remaining at least two m away from the animals and moving slowly I could usually make observations without disturbing them. Jordan and Burghardt (1986) deal quantitatively with some issues of the observer effect on black bears.

It was not possible to take detailed notes underwater. My field notes are biased, not only by which animal's behavior was recorded, but also by which behaviors I selected to record or was able to recognize. Thus, the number of times these behaviors are indicated as occurring in the catalog are only approximations (underestimates) of their true frequencies. Neither copulation nor nesting was ever observed in the field; surely many other, perhaps less conspicuous, behaviors are also absent. I attempted to record all social interactions which precluded recording the sequential behavior of a single individual in a group.

Small juvenile *Pseudemys nelsoni* were seen mostly in areas unsuitable for observations. While both juvenile and adult *P. floridana* were found in deeper water, they panicked more readily and interacted less frequently than did adult *P. nelsoni*.

Basking Observations

Forty three hours were spent recording the behaviors of basking turtles. Three basking logs in the study area offered good conditions for observation. One log, near a bank, was observed from a canoe stationed at the other bank, about 25 m away. Most of the turtles basking on this log were male or small females as it was too narrow for large females to surmount. A second log, near the first, rested partly on the bank and was wider but much shorter. It held up to five large turtles. The third log was near the opposite bank and partially surrounded by cattails. It could be observed from land, about 17 m away,

without disturbing the turtles because the forest served as a natural blind. This log was used by adults and juveniles.

Basking observations were made only on sunny days with the aid of 7 x 35 binoculars. Data were taken by hand using focal animal sampling (Altmann, 1974) on the first adult emerging on the basking site once preparations were made. The behaviors of other basking turtles were recorded if this did not interfere with data collection on the focal animal. The distributions of hours of observation by time of day and month of year are given in Figure 1.

Other Field Observations

At the Rock Springs run study site, opportunistic observations of animals in the water were occasionally made from a canoe, dock, or riverbank. At Payne's Prairie, some behavioral data were collected from a canoe or dike.

Laboratory Observations

Not all age classes of *Pseudemys nelsoni* could be observed in the field. Neonates and juveniles less than three or four years old frequented shallow water with considerable debris and vegetation, barring observation. Thus, their behavior was examined in the laboratory. A pair of adults also was brought into the laboratory to examine courtship in greater detail (Kramer and Fritz, 1989). The behavior of adults in captivity demonstrated the importance of field observations. Important social behaviors, e.g., male-female aggression, were never seen in the laboratory whereas others, e.g., courtship, occurred much more frequently in captivity than in the field.

Four juvenile *Pseudemys nelsoni* were hatched in Aug. 1982 from eggs laid by two captive females. They were maintained in a polystyrene container measuring 122 x 70 x 48 cm for 3 yr and then transferred to a 180 x 39 x 33 cm aquarium. In addition to the juvenile *P. nelsoni*, two juvenile *P. concinna suwanniensis* and three juvenile *P. floridana peninsularis* were maintained in the aquarium. Behavioral data were collected by hand using checksheets or taking notes, and with about 10 min of Super-8 film and 4 h of videotape.

Adult *Pseudemys nelsoni* and *P. floridana* were maintained in the laboratory at various times, some in a circular swimming pool (137 cm diameter, filled to a depth of 23 cm), others in a 180 x 39 x 33 cm glass aquarium. These were three female and one male *P. nelsoni* and two female and two male *P. floridana*, each held for about nine months. About 5 min of Super-8 mm film and 10 h of videotape were taken on a pair of *P. nelsoni* maintained in the glass aquarium.

The behaviors of captive animals were noted along with any changes over time. The videotapes and Super-8 mm films were useful for examining details of courtship, feeding, and basking behaviors.

Coverage

The sample coverage and repertory fraction (Fagen and Goldman, 1977) were not calculated because poor observation conditions and limited data recording techniques in the field assured biased samples of behavior. Additionally, behaviors were known to be missing, e.g., copulation.

Fagen and Goldman's (1977) methods of calculating catalog completeness require that behavior is sampled randomly. While the problem of missing categories does not pose

difficulties (Fagen and Goldman, 1977), biased sampling would make calculations of catalog completeness meaningless.

Emotional Behavior

Izard (1982) suggests that an understanding of emotional processes should be addressed at three levels: biological (neurophysiological-biochemical), behavioral (expressive), and subjective (experiential). An emotion is defined using data from all three levels, however, data from just two should be sufficient for identification (Izard, 1982). Emotional behavior in animals would be difficult to research from the subjective level. Since I have no data at the biological level, my perspective is necessarily speculative and anthropomorphic. In describing emotional behavior I have considered overt behaviors and context simultaneously although Lewis and Michalson (1982) caution that, due to variation, the emotional behavior of individuals may differ in similar contexts. The classification that I give is intended to suggest situations where emotional behaviors are reliably observed and to group situations involving the same emotional behavior. Labeling was conservative and reflects terminology used frequently in the literature.

The terms emotion and emotional behavior are difficult to define, in part because they blend with feelings on one level and motivation on another, and in part because clear distinctions among emotions have largely proven refractory at the physiological or neurophysiological level. For this ethogram I propose the following definition of emotional behavior: An abrupt change in behavior pattern, often reliably elicited by certain classes of temporally unpredictable stimuli, such as the behavior of conspecifics or potential predators, and resulting in a presumably adaptive response. This does not extend to behavior patterns exhibited due to regular cyclical exogenous or endogenous changes,

e.g., foraging to satisfy hunger. Interpreting emotional behavior in turtles is also difficult because there may be little selective advantage for expressing certain emotions (e.g., pleasure) to conspecifics, thus little outward manifestation of a change in mental state.

CHAPTER 3

RESULTS

Behaviors of *Pseudemys nelsoni*

Aquatic Behaviors

In the catalog that follows aquatic behaviors are grouped, for convenience, by presumed function. The relationship between functional and simplified contextual categories of *Pseudemys nelsoni* is diagrammed in Figure 2. Events (behaviors completed in a short time, on the order of seconds) and states (behaviors whose usual duration is on the order of minutes or hours) should be readily distinguishable from the description. Some formations (orientation of one animal with respect to another, Phillips, 1977) are given. Many of the descriptions fit *P. floridana* and *P. concinna* well; differences that I observed are noted. The behaviors described below are listed with frequencies and percent of total time from field data in Appendix 2. Total recorded frequencies of behaviors and observation times in the field are as follows: male *P. nelsoni*, 1070 behaviors, 40.3 h; female *P. nelsoni*, 565, 26.1 h; male *P. floridana*, 283, 13.1 h; female *P. floridana*, 492, 22.5 h. The actual number of individuals observed during the study is not known since most individuals were unmarked. I estimate that observations were made on 200-300 individuals.

The likelihood of observing male and female *Pseudemys nelsoni* (Fig. 3) did not differ throughout the day. I tested this by subsampling the data set, assigning months of observation randomly to one of two groups. An analysis of variance was performed with

percent time observed as the response variable and sex and time period as the independent variables (Table 2). This analysis relies on several assumptions not completely met by these data. Violations include bias introduced by observing some individuals on many occasions and others on far fewer, and by confounding the error term with a possible seasonal effect. However, the purpose of this analysis was exploratory rather than definitive. None of the effects (sex, time period, or sex by time period) were significant at the 0.05 level suggesting that the sexes were equally likely to be observed in any of the time periods and that time period did not affect the likelihood of seeing animals.

Foraging

1. Eating. Behaviors associated with the processing of food prior to digestion. Ingesting large items begins with a forward thrusting of the head with a concurrent opening of the jaws, concluding with a bite. The bite is completed even if the animal misses the food item. If small, the food item is swallowed whole. If too large to be swallowed whole, it is manipulated by pushing or tearing with the forefeet (see below) or by releasing, then regrasping the item, after shifting its head.

Turtles eating *Oscillatoria*, the most frequently consumed food, stand on the substrate facing a small mass of algae. The jaws are placed into the algal mass, opened slightly and the hyoid apparatus is lowered after which the jaws are closed and the hyoid raised. This sequence occurs repeatedly giving the appearance of very small nibbles.

2. Swallowing. Food is moved posteriorly from the buccal area.

3. Tearing food with forefoot. The food item is held with the mouth, a forefoot is rotated so that the palm faces outward and then raked against the food. This may be performed with one forefoot or both forefeet simultaneously.

4. Expose food. The turtle hovers (tread-paddle) over the potential food item, rotates the front feet, palms facing outward, brings the front feet together above the food item, then gently brushes outward with the front feet removing the debris covering the food item.

5. Food contest. One animal attempts to eat food held by another. When the animal grasping the item was larger than its contender it would often retract its head slightly, swing its forelimb(s) forward with the palm(s) outward and push, usually catching the other turtle's head, pushing it away.

Approach/Investigate/Avoid

1. Approach (Figs. 4 and 5). An animal moves toward a conspecific, observer, etc. with the apparent goal of attaining it.

2. Follow. Following is approaching an animal that is moving away slowly (walking or swimming).

3. Nose (Fig. 5). Animals place their nostrils within a mm of the surface of an object or conspecific.

4. Turn toward. The entire body is rotated, requiring the coordination of all four limbs to orient to another individual. The head of the animal is usually directed toward it before turning.

5. Avoid. A) An animal moving toward or near another abruptly changes direction, moving around or away from it. B) An animal that is approached by another moves away from it before the approaching animal is within one body length.

6. Leaving. An animal leaves the immediate vicinity of another following investigatory behavior or an interaction, but not due to the quality of the interaction (does not include fleeing or retreating).

7. Nosetouch (Fig. 5). Two animals in close proximity and within 90° of facing each other slowly extend their necks fully until their snouts touch or almost touch.

Comfort Movements

1. Coughing. The animal closes its eyes, opens its mouth and the partially retracts its head. Then it drops its head while at the same time retracting it slightly in a jerky manner. The head is then slightly raised and extended. This is repeated several times.

2. Rubbing/scratching. A) Back rub. The animal crawls or wedges under an object (rock or hose in the lab), pushes up to exert some pressure against the object with its carapace, and swivels. B) Head rub. The head is partially retracted and bent in the direction of one of the forelimbs. That forelimb is rapidly rubbed back and forth over part of the head (Fig. 4). C) Both forelimbs and hindlimbs may be rubbed against the underside of the marginals. D) The hindlimbs are occasionally rubbed against each other or (E) against the tail (Fig. 4).

3. Yawning. The mouth is slowly opened very widely for one or two seconds, then closed quickly.

4. Stretch rear leg. A rear leg is slowly extended laterally and posteriorly while the digits are simultaneously spread. The leg is withdrawn more abruptly. The timing and appearance are similar to that of a cat performing the same behavior.

5. Limb shake. The limb is partially extended and the distal portion rapidly shaken. This act is similar to rubbing but the appendage does not touch the body.

Locomotory

1. Swimming (forward). Forward locomotion through the water above the substrate. There are three readily distinguishable classes of forward swimming, based on speed.

The slowest, paddle-glide, has noticeable interstroke pauses (glides). The animal appears to be unhurried, often moving its head from side to side, giving the impression that it is scanning the environment. The directed paddle is variable in speed but directed toward a specific object. The head is normally outstretched and oriented toward the object. There are no or infrequent glides between strokes. The escape dash is directed away from an animal (usually the observer) at maximum speed.

2. Backpaddling, turning and stopping. Locomotion in the water other than swimming forward. Swimming backwards or backpaddling occurs by a sculling motion of the hind legs alone and is slow. Turning usually involves the forelimbs as well. Movements involving turning are generally well coordinated, better on the horizontal than vertical plane. The hindlimbs are used for stopping. Turtles are able to stop and turn quickly during paddle-glide and directed paddle.

3. Tread-paddle. While the hindlimbs are backpaddling, the front limbs paddle forward. The head and tail are extended. The animal remains stationary in the water.

4. Walk. Locomotion on the substrate. The plastron is usually not in contact with the substrate.

5. Burrowing. An animal burrows into the substrate so that mud covers it to at least the carapace marginals.

Agonistic

1. Stare. An animal faces another within two body lengths, looking steadily at its head. This was considered a threat because the recipient usually looked, turned or moved away. This behavior has been noted in other taxa (Exline, 1982).

2. Look away. An animal appears to avoid looking directly at the head of another individual in close proximity. This behavior has been described by various authors for

other species of turtles (Boice, 1970; Bury et al., 1979; Lovich, 1984) and is an example of a "cut- off" behavior (Chance, 1962).

3. Nudge. One animal, with its snout, lightly pushes against another.

4. Gape (Fig 6). Gaping, interpreted as a threat, occurs when one animal, facing another, partially retracts its head and rapidly opens its mouth. The duration of a gape is variable but usually several s.

5. Snap (Fig. 6). The head is thrust forward with the jaws open, as in a bite, but the jaws close far short of the other turtle. These turtles have poor aim and may miss even a stationary food object on the first attempt. Some snaps, however, fall at least 10 cm short. This seems in excess of what might be attributable to poor aim.

6. Social bites and attempted social bites. Bites (as described above in eating) or attempted bites that were directed to other turtles were considered to be social bites.

7. Withdrawal of head and front limbs (Fig. 7). Retraction of head and front limbs under carapace.

8. Extension of head and front limbs (Fig. 7). An animal extends most or all of its head and front limbs.

9. Tail extension. Tail parallel with body axis, either straight or curved ventrally.

10. Tail retraction. Tail is withdrawn sideways underneath carapace.

11. Complete retraction. All limbs, head and tail are withdrawn under the carapace.

12. Retreat. The individual moves backwards rapidly away from another animal for roughly one to three body lengths by crawling or swimming. It then stops or turns and swims away. The head is partially retracted.

13. Chase (Fig. 7). An animal attempts to approach another that is rapidly swimming away.

14. Push (Fig. 7). One animal attempts to change the position of another, either by pushing it with the front of the carapace (male- male) or by pushing it forward with its whole body while holding the other turtle's forelimb in its mouth (male-female).

15. Drag. A turtle, either biting or being bitten by another, changes its position and by so doing displaces the other by pulling it behind.

16. Circle. A) One male swims around a second male, pivoting on the bottom and maintaining a head-to-head orientation. B) Both males swim, circling each other, maintaining a head-to-head orientation.

17. Lateral presentation. An animal changes its orientation so that its side is presented to the other turtle.

18. Tilt body (Fig. 7). The shell is tilted vertically to about 45° and tipped down slightly anteriorly in response to an approaching conspecific male. The male is presented with the top surface of the carapace. The behavior occurs on the substrate.

19. Kicks. One animal pushes another away with several sharp kicks to the other's carapace using a hind leg.

20. Grip (Fig. 7). One individual holds another with its jaws. This occurred only when a male gripped a female's forelimb.

21. Yanking. A male pulls a female's foot with his jaws while pushing or holding the female's shell away with his front legs. This is repeated rapidly in short bouts sometimes producing a clattering sound (see below).

22. Clattering. A clack, produced when the male's front carapace contacts the bridge area of the female's shell, occurring when the male stops yanking on the female's forelimb. The female may also try to retract her front leg, increasing the force with which the shells come into contact. This behavior was repeated frequently and quickly, producing a

clattering sound with up to 10 clacks/bout. Up to seven consecutive bouts of clattering were observed with about one bout/min.

23. Perpendicular arrangement of shells (Fig. 7). During male-female agonistic interactions the shells are roughly perpendicular. This formation persists as long as the male is biting the female's forelimb.

24. Face same direction- head to tail (Figs. 5 and 7). This position often delineated the beginning and sometimes the termination of a male-male agonistic interaction. This formation also occurs in the initial stages of courtship (Fig. 5).

25. Face opposite direction- head to head. This was the usual position in a male-male interaction, attained shortly after its initiation. Males might circle each other or move backward or forward while maintaining this formation.

Sexual

1. Swim above (Figs. 5 and 7, see also Fig. 1 in Kramer and Fritz, 1989). One turtle swims above another orienting to its head and attempting to position itself for titillation. The turtle above attempts to maintain an inclination of approximately 20°, tipped downward anteriorly, and extend its forelimbs anteriorly.

2. Rotate forelimbs. The forefeet are brought forward together and rotated inward (pronation). The motion concludes with the forelimbs roughly parallel to the head, extending forward with the palms facing outward.

3. Titillation. The digits of the forelimbs are vibrated rapidly, with the claws placed just above another turtle's head.

4. Mounting (transition to copulation). The male moves from the swim above position to the copulation position (described in Kramer and Fritz, 1989) by sliding backwards, bringing the rear of his plastron in contact with the rear of the female's carapace.

5. Copulation. This behavior was not observed in the course of this study but is described by Kramer and Fritz (1989).

Miscellaneous Maintenance Behaviors

1. Throat pulsation. The throat rhythmically distends and contracts, due to lowering then raising the hyoid apparatus. This draws water through the nostrils and out the mouth, which is slightly opened at the same time that the hyoid apparatus is raised. The flow of water can be reversed to exit from the nostrils.

2. Surfacing and submerging. Animals come to the surface to breathe, either extending the head or only the nostrils above the water surface.

3. Defecation. Voiding of feces.

4. Urination. Voiding of the bladder.

Startle/Escape

1. Startle response. The immediate reaction to a potential predator.

An animal in the water, startled head-on by an observer, withdrew its head, forelimbs and tail, and used its hindlimbs for stopping and backpaddling. If startled from behind the turtle withdrew its tail and rapidly swam away. This act was completed in one s or less.

2. Wedge under an object. A hatchling or small juvenile swims to the bottom where it attempts to burrow into the substrate or wedge under an object.

Inactive

1. Rest. Animal is alert but inactive.

2. Ride and resting on others at surface. A smaller individual uses a larger one that is swimming slowly or resting near the surface as support.

3. Resting on others on bottom. One turtle crawls or rests on the carapace of another on the substrate. It differs from mounting (sexual behavior) because the animals are not necessarily facing the same direction and the turtle resting on the other does not subsequently exhibit sexual behavior.

4. Waterbasking. The animal is supported by debris or vegetation at the surface in full sunlight. The head and most of the carapace are out of water, the limbs are lowered and the tail extended.

5. Rest in substrate. The animal is inactive and in mud with only the head and carapace visible (see burrowing).

6. Sleeping. Animals are inactive and eyes are closed for long periods of time.

Basking Behaviors

Basking observations were conducted using focal animal sampling (Altmann, 1974), supplemented by noting the behaviors of others when the focal animal was inactive. Data on focal animals are analyzed and presented in Part 3. Subtle behaviors were mostly recorded only for the focal animal. Most turtles observed basking were male *Pseudemys nelsoni* (814 behaviors noted). The number of behaviors recorded for the three other groups are: female *P. nelsoni*, 371; male *P. floridana*, 45; and female *P. floridana*, 61. The basking behaviors of the small sample of *P. floridana* observed did not differ from that of *P. nelsoni*.

Social

1. Nose/nudge. A turtle behind another, facing the same direction, noses/nudges the tail or carapace of the one in front.

2. Climb/rest on another. One animal partially climbs on another and rests with the front of its plastron supported by the other turtle's carapace.

3. Touches. An animal contacts a second by placing a limb on its carapace.

4. Push off. A hindlimb is used to push off an animal that has touched or begun resting on its carapace.

5. Swivel. The shell is elevated slightly and rotated back and forth about 45° after tactile stimulation from a second turtle.

6. Push with shell. A larger animal pushes a smaller animal with the edge of its carapace.

7. Bracing. An animal that is pushed resists being moved by extending its legs down and laterally as far as possible, clutching at the substrate with all four legs. This occurred if the turtle nosed/nudged was unable to move forward.

Nonsocial

1. Emerge from water. *Pseudemys nelsoni* follows the emergent pattern described for *Trachemys scripta* (Auth, 1975). Animals appear wary or hesitant when approaching a basking site. Once begun, the animal rapidly mounts the log. When on top it usually turns 90° so that its body axis is parallel to the log. The front legs are used to pull the animal up to the point where the hind legs can grip the log. If at least one hind leg cannot be brought into play, the animal is not capable of emerging.

2. Into water. An animal moves into the water by walking or pushing off and dropping in. Sometimes animals were pushed in by others or fell off when moving about on the log.

3. Turning in position (rotation of Auth, 1975). An animal changes orientation without moving forward or backward. The plastron may or may not be elevated above the substrate. When turning in position the hindlegs were more important than the forelimbs for grasping the substrate. After emerging turtles usually turned 90°.

4. Kicking. A limb is rapidly retracted then extended several times. The motion appears similar to swimming movements and is made in a horizontal plane but is performed more quickly.

5. Moves legs. One or more appendages makes a slow swimming or waving motion, not contacting the substrate and usually not repeated more than once.

6. Rubbing. An appendage is rubbed against another body part or substrate. Five readily distinguishable kinds of rubbing were noted; rub head with forefoot, rub anterior undersurface of carapace with forefoot, rub posterior undersurface of carapace with hindfoot (lateral and anterior to hindfoot), rub tail and undersurface of carapace above tail with hindfoot, and rub appendage against the substrate.

7. Limb retraction and extension. Retraction occurs when a limb is folded next to the body, under the carapace. Extension occurs when a limb is straightened. The hindlimbs are extended laterally and posteriorly, the forelimbs laterally and anteriorly. They may be touching the substrate but usually are lifted so that the feet are slightly elevated.

8. Raises/lowers limb. The limb is elevated from the substrate, remaining partly flexed. An appendage can be lowered from a partly flexed, retracted or extended position.

9. Raises/lowers head. The head is elevated or lowered, the neck remains slightly flexed. When lowered the neck is usually partially retracted and the head parallel with the opening between carapace and plastron.

10. Shake head. The head is moved very rapidly and briefly from side to side in the horizontal plane.

11. Scan. The turtle elevates its head and turns it from side to side slowly in a horizontal plane.

12. Walking. Terrestrial locomotion (discussed in detail by Walker, 1979). On land or a basking site animals have two readily distinguishable gaits; a very slow deliberate walk, with frequent pauses, and a rapid, escape gait.

During walking the head is lowered, the neck parallel to the substrate, and the body is held completely off the log or ground. Stops are frequent. After stopping the head is raised and the animal scans.

In the escape gait animals move as quickly as they can, usually toward water. The head is completely or partially retracted.

13. Inactive. Animal is quiescent, eyes may be open or closed. Animals do not commonly remain still for more than 15 min.

14. Nose substrate. The animal brings the tip of the snout near the substrate.

15. Digit spreading. The digits are widely separated so that the webbing is extended.

16. Yawn. The animal opens its mouth very widely and slowly then closes it. There are no discernible difference from yawns in the water.

17. Nonsocial gape. The animal opens its mouth to a lesser extent than in a yawn but leaves it open, usually for 15 or more s. The open mouth is not oriented to another turtle.

Miscellaneous Behaviors

Behaviors included in this section were either known to be missing (nesting) or did not fit into other categories (hiss).

1. Hiss. Sound is produced as air escapes through the nostrils and possibly the mouth during retraction. Hissing was heard when the animal retracted suddenly on land.

2. Nesting. No animal was observed nesting.

Emotional Behavior

Emotional behaviors are subjectively labeled fear, annoyance/anger and pleasure. Nonspecific arousal is also described, although it is probably not an emotional behavior, because it could be distinguished from other emotive or motivational states and, in particular situations, has been treated as an emotional behavior (e.g., Plutchik, 1980; for other authors see Fantino, 1973).

These emotions are characterized below. It should be borne in mind that this list is likely a simplification of the emotional behavior of these animals.

1. Fear. In water an animal backing away and fleeing, or turning and fleeing manifests fearful behavior. Other indications of fearful behavior are retraction into the shell and defensive gaping to an approaching conspecific. These animals always have their tails withdrawn.

2. Anger/annoyance. An animal stares at (threatens) another individual (contrasting with the look away posture) and is liable to gape, snap or bite at it.

3. Pleasure. Behaviors similar to those of other taxa in contexts that appear pleasurable, e.g., the slow, almost lazy opening and closing of the eyes and general relaxation and extension of the limbs during a basking episode when the animal first positions itself under a warm lamp. This emotional behavior is less obvious than the others.

4. Nonspecific arousal. The individual is very active, either A) excited, or B) agitated or restless.

A) Excited. An animal engages in vigorous swimming directed or pertaining to food or another individual (in a courtship or courtship-like context).

B) Restlessness. An animal ignores other individuals and objects and swims continuously, punctuated only by surfacing for air.

Behaviors in Context

Aquatic Behaviors

Foraging

Most animals were seen feeding from afternoon until dusk in open, often shallow areas where *Oscillatoria* spp. was abundant. The top of the algal mass alone was grazed. Only a small amount of each algal mass was eaten before moving to another patch without backtracking, males moving more often than females. They occasionally ate *Oscillatoria* spp. or vegetation at the surface but not in long feeding bouts. Foraging appeared to be solitary although two turtles were sometimes seen within one m of each other, probably a result of the distribution of food resources.

The following natural foods were consumed: *Oscillatoria* spp., *Hydrilla verticillata*, Eel-grass (*Vallisneria americana* and/or *Sagittaria kurziana*), Spatterdock (*Nuphar luteum*) flower bud, and an apple snail shell. In addition, a female *Pseudemys floridana* ate an old Spatterdock stem. A bromeliad that had fallen into the water was bit but rejected. Lettuce and celery tied to a branch were also rejected. In the lab the following foods were accepted: dog food, cat food, lettuce, anise, celery, crickets, dead minnows, Plaster of Paris briquette, algae (unidentified), and feces (of other turtles). There were no observable differences in the feeding behavior or food items consumed between *P. nelsoni* and *P. floridana*. The nibbling behavior seen when turtles ate *Oscillatoria* may function to strain the water entering the mouth of coarser particles. Alternatively, it may be similar to the phytophagous behavior described for other species (Belkin and Gans, 1968).

Swallowing always occurred in the water. The animals used inertial feeding to initiate the process. It is likely that water pressure built up anterior to the food item is used to assist the passage of food through the esophagus.

The effect of tearing depends on the food stuff. An insect usually comes apart after several seconds, especially if caught by the claws. A fish is twisted so that its long axis is parallel to that of the turtle. Pieces of plant matter are usually separated by tearing. If several tearing attempts are unsuccessful the turtle relinquishes its hold and bites the food item elsewhere. After tearing there may be small food particles left on the front claws. The particles are not brought to the mouth, instead the turtle extends its head to its claws to eat them.

During a food contest it was not clear if the turtle gripping the food was attempting to push away the other turtle or tear at the food. The recipient might attempt to appropriate the item again but would never gape or bite in return. Individuals also chased others grasping food. Possibly, the food item alone was being chased. These behaviors were seen only by juveniles in the lab when eating animal matter. Turtles consuming plants would feed next to each other without interacting.

Approach/Investigate/Avoid

Most approaches and investigatory behaviors, other than toward the observer, were directed toward conspecifics. This suggests that species discrimination is possible from a distance, at least in the relatively clear water of a spring run (see below).

While making observations I was frequently approached when an animal was swimming downstream and I was in or near its path. Occasionally, an animal appeared to go out of its way to investigate me, some individuals repeatedly during an observation

session. A behavior similar to exposing food was performed by a male *Pseudemys nelsoni* in the field after it had approached me, for no apparent reason.

Individuals usually approached the observer, some inanimate objects, and another turtle's posterior or side slowly and hesitantly. If the approached individual was at the surface, the approaching turtle stopped behind it and extended its head while treading water or resting on a branch.

An animal approached the anterior of another slowly or rapidly. In the lab, a slow approach was seen in juveniles preceding a titillation sequence. The approach was usually made by swimming. *Pseudemys concinna* juveniles differed in that the slow approach to the anterior of another usually preceded an aggressive interaction. In general, animals avoided approaching each other head-on. Rapid approaches occurred during courtship patterns (juvenile or adult) when the recipient dodged or fled. When it stopped, the displayer approached it very rapidly. Rapid approaches were also common in aggressive encounters.

Sufficient approaches were observed for statistical comparisons between sexes using the G-test. Male *Pseudemys nelsoni* approached both conspecific males and conspecific females significantly more frequently ($p < 0.05$) than did female *P. nelsoni*. While male *P. floridana* approached female conspecifics significantly more often ($p < 0.05$) than did female *P. floridana*, neither class approached conspecific males or *P. nelsoni* of either sex. Male *P. nelsoni* were not observed to approach male *P. floridana* but did approach female *P. floridana* suggesting that male *P. nelsoni* had greater difficulty distinguishing between conspecific and heterospecific females at a distance than did male *P. floridana*. This could not be tested statistically because opportunities for social interactions were unknown. Assessing opportunities would have required determining the proportion of these two species in the study site as well as the degree of microhabitat overlap.

I have not seen following where two animals, moving in the same direction, remain the same distance apart. Sequences when one animal follows another culminate when the animal being followed is reached.

Obvious avoidance behavior to other turtles was uncommon. Only males were avoided. This behavior was not common in *Pseudemys nelsoni* and not observed in *P. floridana.* I was usually avoided and never used as a resting platform.

Leaving was the usual termination of an interaction. The animal that was leaving would usually look away from the other before leaving.

Nosing is presumably for olfaction, most often addressed to potential food items or other turtles. In a social context the cloaca, hindlimbs or head of the other turtle was nosed. Nosing the substrate sometimes occurred after an animal settled to the bottom.

Nosetouching was maintained for 5-10 s. One animal broke contact by turning its head away. This was not often seen in the field. On one occasion an interspecific nosetouch was observed between a female *Pseudemys nelsoni* and a female *P. floridana.* Nosetouching was performed more frequently by juveniles in the lab. It never ended in an agonistic encounter or titillation sequence in juvenile *Pseudemys nelsoni* or *P. floridana* but in *P. concinna suwanniensis* it sometimes ended with a gape or snap. The function of this behavior is not clear. It may serve to gather information on the other turtle or be a 'greeting'.

Comfort Movements

During coughing, my impression was that the animal was trying to expel food from its throat although this was never observed. This behavior was infrequent, usually following eating. It may aid in manipulating food in the throat to assist swallowing.

Rubbing was usually a vigorous behavior. Backrubbing may be done for periods of 10 or more minutes with interruptions for breathing. The function of this behavior may be to aid in dislodging epidermal layers of the scute during ecdysis.

Yawning was sometimes accompanied by rubbing the head with one of the forelimbs. It did not occur following eating as seen in many lizards and snakes. No external stimulus appeared to initiate yawning.

Limb shaking may be performed to rid the appendage of an irritant or, with stretching, to stimulate circulation.

Other than coughing, comfort movements usually occurred when animals were resting on the bottom and appeared to be relaxed. These movements were seen infrequently in the field and do not greatly differ from similar behaviors in basking animals. None appear to have a social signal value.

Locomotory

Both species of turtles swim slowly and can be captured easily by hand underwater. *Pseudemys floridana* are stronger swimmers than *P. nelsoni* and females of both species are slower than conspecific males. When attempting to escape, adult *P. nelsoni* swam in a large semicircle close to the surface even though individuals were observed feeding at the deepest point in the study site (about 5 m). In contrast *P. floridana* would flee toward deeper water along the bottom. Juveniles of both species fled to the bottom.

The paddle-glide swimming gait was used mostly by solitary individuals. In the lab the directed paddle was used for approaching a food item and, sometimes, another individual. Following the escape dash, some animals turned their heads to see if they were followed. In the field, tread-paddle was exhibited mostly by *Pseudemys floridana* females when they surfaced for air and lasted less than 30 s.

While swimming adult turtles are negatively buoyant. When they stop swimming they slowly sink to the bottom. Contact with the bottom substrate is usually made first by the downward projecting hind limbs. Animals walk only short distances, as when moving from one food patch to another. Both aquatic and terrestrial gaits in chelonians are discussed in detail by Walker (1979).

Burrowing was seen infrequently at the Rock Springs run study site and not employed as an escape maneuver by adults. However, in Payne's Prairie adults did attempt to escape by burrowing. While the substrates in both areas consisted of soft mud, the water was much shallower at Payne's Prairie. Turtles may enter the mud to avoid interactions with other animals or to thermoregulate. Bottom mud is often one or two degrees warmer than the water above it, probably due to the presence of decaying organic matter.

Agonistic Behavior

The function of look away is probably to avoid initiating an interaction with a facing individual. An animal seeking to interact with another makes no attempt to look away from the individual it is approaching. An animal that is approached may try to look away from one approaching by looking to the side, down or nosing the substrate, or turning away. The appearance of indifference to other individuals may be the result of this behavior.

Gapes were frequently seen in agonistic interactions. In melanistic males, the open mouth, with its light pink interior, sharply contrasts with the black head. The recipient's usual reaction to gape was retreat (backing up). In the lab this behavior was performed more frequently by juvenile *Pseudemys concinna* than juvenile *P. nelsoni* and never by juvenile *P. floridana*.

Biting was not observed with great frequency in agonistic interactions although poor observation conditions may have precluded seeing nips. Biting did not seem to inflict damage on conspecifics, even after a prolonged biting sequence.

Occasionally a retreat began with a jerky appearance. This was due to the repeated synchronous retraction then extension of the head and forelimbs. At the same time the animal moved backward using its hindlimbs alone. It appeared to be a conflict behavior (approach/withdrawal). Retreat sometimes occurred without any overt sign of aggression by another turtle.

Male-male agonistic interactions were usually initiated when one male disturbed another at the surface by nudging it. In some cases this may have been augmented by a nip or be peculiar in some other way because the recipient immediately turned around to face the animal that disturbed it. When I poked males resting at the surface with a pencil or my finger on a hind limb there was either no response or the animal would panic. Some aggressive interactions began when a swimming male encountered a stationary one. Aggressive interactions were infrequent, in most encounters males either ignored each other or exhibited only a cursory interest in the other.

After being nudged or bit the male at the surface would usually submerge backwards and turn to face the male that disturbed it. They would face (stare at) each other for five or more seconds. The only physical trait that appeared to be associated with aggressive behavior was melanism in males; this also appeared to be the case in male-female aggressive behavior.

My impression of aggressive interactions is that aggressors or dominant males exhibited the following behaviors: the initial nudge/bite, gape, snap, stare, tail extended, head and forelimbs extended, approach, chase, and circle. Submissiveness was indicated by look away, withdraw head and forelimbs, retract tail, and retreat. Defensive behaviors

included withdraw head and forelimbs, circle, gape, and tail retraction. These defensive behaviors were observed in more protracted encounters and seen sporadically in both animals.

Fights were of short duration and usually ended abruptly, one animal either fleeing or, more commonly, surfacing. Occasionally the individual at the surface would be nudged/bit again and another agonistic interaction would ensue. Usually both males would surface without further agonistic behavior. In most cases clear winners and losers were not discernible, making interpretation of the fights difficult.

In the field male-male chases sometimes followed agonistic interactions. The longest chase was less than two meters. In laboratory juveniles, chasing occurred in sequences of precocial courtship.

Two aggressive interactions were unusual. In one, after the initial nudge, staring and subsequent circling the males descended to the substrate and appeared to be pushing against each other, carapaces abutted, head and forelimbs partially withdrawn, and gaping (Fig. 7). Similar behavior has been described for combating male tortoises (Carpenter and Ferguson, 1977). One male surfaced for air during the interaction. While there the other male remained motionless on the bottom until the first returned, the fight seemingly picking up where it left off. In the second unusual aggressive interaction, a group of four or five males remained in close proximity to each other for at least 10 min while carried along by the current. Most or all of the animals were intermittently engaged in agonistic interactions with different individuals in the group. When the group dispersed there were no clear winners or losers.

In summary, male-male agonistic behavior was uncommon although groups of males were often seen. Fighting could best be characterized by staring and gaping leading to quick but unclear resolutions. No bites other than the initial nudge/bite (nip) were seen,

unlike male-female aggression in this species and *Trachemys scripta* (Rundquist, 1985) and male-male aggression in *T. scripta* (Lardie, 1983). No male-male aggression of any kind was seen in *Pseudemys floridana.*

Only one kind of agonistic behavior was observed between males and females underwater, and it occurred infrequently. Melanistic males were the initiators and aggressors. A male attacked a female by grasping a forelimb with his mouth while the female was resting at the surface or after chasing her down. The male would try to pull the female to the bottom by swimming backwards, the female trying to resist and free her forelimb. If the female was unable to do so the male pulled her to the bottom and started tugging on her forelimb, repeatedly tearing and pulling as if to separate the female's limb from her body. Tearing may be a response to holding an object too large to be swallowed held in the mouth. After several minutes the male would release the female and she would swim away. The male never tried to pursue the female or exhibited sexual behavior. A female encountering a male on the substrate sometimes tilted her body, probably to discourage male aggression. Captive individuals may perform this behavior if they are tapped with a pencil on the anterior edge of the carapace while basking.

Male aggressive behavior by a male to a female *Pseudemys floridana* may have occurred once, but this is questionable due to poor observation conditions. In this encounter, a male nudged or nipped a female several times during a courtship episode.

No agonistic behavior was ever observed between adult females in the field. Juvenile females in the lab occasionally exhibited agonistic behavior, usually to ward off another preparing to display (titillate). This was always followed by the approaching animal retreating.

Sexual

Although male *P. nelsoni* investigated both conspecific and heterospecific females, they appeared much more likely to investigate conspecific females. This could not be tested statistically because the ratio of abundances of females of the two species was not known.

Male *Pseudemys nelsoni* only courted female *P. nelsoni.* However, on one occasion a female *P. floridana* swam between a pair of courting *P. nelsoni* and the male started to follow her. In less than 30 s he stopped, turned back, and appeared to search for the female *P. nelsoni.*

Since I did not catch courting animals, I cannot document the degree of melanism or other characteristics possessed by courting males. My impression was that courting males tended to be smaller than average and not be strongly melanistic.

Courtship appeared to be a time-consuming behavior, lasting many minutes, hours, or even days with animals covering large distances. Typically, a male overtook the female, titillated, fell behind and followed. When the female surfaced for air, the male surfaced immediately behind her. As soon as she submerged, he submerged, followed her, and started a new cycle. Titillation occurred only when the female was moving and when the recipient's head was under water. A bout of titillation probably averaged fewer than 10 vibrations. Courtship sequences contained many bouts of titillation.

No instances of interference were seen by other males or females except for the mix-up described above. Courtship is analyzed in greater detail in Kramer and Fritz (1989).

Courtship in *P. floridana* was similar to that of *P. nelsoni.* The percent of observed time courting appears disproportionately large in *P. floridana* (Appendix 2) due to observations made on two long courtship sequences (totaling 69 min). The swim above formation was seen only during adult and precocial courtship.

Miscellaneous Maintenance Behaviors

The probable function of throat pulsation is to create a water current as an olfactory aid. This behavior is more or less continuous whenever the turtle is active in the water. Juvenile *P. concinna suwanniensis* can enlarge their throats to a greater extent than can juvenile *P. nelsoni* and *P. floridana.*

Animals surfacing sometimes shake their head slightly two or three times while extending it above the surface. This may prevent debris on the water surface from sticking to their eyes. A functionally analogous behavior, but with the use of the forefeet, has been described for *Trachemys scripta* (Auth, 1975).

Submerging may be slow, by sinking, or rapid, by backpaddling. Animals submerge rapidly when panicked but also sometimes when there is no obvious disturbance.

Defecation occurred most often in the water when the animal was alone, foraging or resting. There was no obvious preparation except for a slight lifting of the tail. The feces are very soft and separate easily. Urination cannot be observed while the animal is in water. Wild or captive animals frequently urinate when handled.

Startle/Escape

These behaviors were given only in response to my presence and never to another turtle. The first reaction of any startled animal was to retract its head and front limbs, at least slightly. *P. floridana* appeared to be more wary and susceptible to panicking than *P. nelsoni.*

Wedging under an object occurred after a small juvenile was alarmed at the surface. It may function to avoid visual detection, resist attempts at extrication, and prevent floating to the surface. For unknown reasons, an adult *Pseudemys floridana* wedged under a log.

Inactive

When floating a resting animal breathes at the surface without support from the vegetation or substrate. All limbs and the tail are extended. The head is out of water and the animal peers about. This behavior normally lasts less than one minute. When supported by the substrate, the position of a resting animal is similar but may be retained for much longer periods. In deeper water, periods of rest on the bottom appear oxygen constrained. *Pseudemys floridana* was observed resting on the bottom for longer periods than *P. nelsoni*.. In the field, animals always appeared alert when resting. They were occasionally found resting in cavities in the bank or burrowed in the mud. In Payne's Prairie a radiotracked male *P. nelsoni* appeared to have remained completely burrowed in about 50 cm of mud for several days. In the lab, juvenile *P. nelsoni* occasionally retreated into a shelter, completely retracted and closed their eyes. They may rest immobile in this posture for many minutes. In the lab, juveniles spent less time resting than adults.

Turtles used as support by others appeared indifferent to this. During courtship in *Pseudemys nelsoni* but not *P. floridana*, the male rested on the female when she stopped and surfaced to breathe. When the female submerged the male often rode until he fell off, then followed her. Riding and resting on others was seen at other times in the field and lab and was not sex specific. Legler (1956) describes *Chrysemys* basking on swimming *Chelydra* (snapping turtles).

Animals were inactive much of the day, usually in a patch of debris or vegetation. Commonly several animals of either or both sexes rested together in a small group. This grouping may be an artifact of the heterogeneous habitat, with preferred resting sites acting to concentrate individuals. Groups were seen near the upstream edge of vegetation patches, underneath vegetation overhanging the bank, and in the vicinity of fallen trees or large branches that had collected debris at the surface.

Although physical measurements of resting sites were not made, preferred sites appeared to differ between the two species. *Pseudemys nelsoni* rested mostly near the bank in shallow water (about 1 m deep) with debris and vegetation. In contrast, *P. floridana* tended to rest in more open, deeper areas but still with some debris and vegetation. However, individuals of both species were found resting in the same group, usually the deeper sites. *P. floridana* individuals also appeared to rest while floating at the surface for longer periods of time than did *P. nelsoni.*

Most individuals seen waterbasking from a canoe were *P. nelsoni.* Judging from the ring of algae around the edge of the carapace in some animals, this posture is probably maintained for long periods of time in favorable conditions.

In the field *P. nelsoni* were found sleeping at night supported by vegetation sufficiently close to the surface to breathe by extending the head above the water. *P. floridana* were seen on the bottom or supported by vegetation but 15 cm or more below the surface.

Basking Behaviors

Preferred basking sites afforded an unobstructed view of the surroundings, typically located more than a m from the bank. These animals were prone to panic when basking. If approached quickly, they often did not leave the log in a directed manner, rather any rapid movement on their part caused them to lose balance and fall into the water. This scurrying motion may startle an approaching predator. If approached slowly their movements are more efficient.

Social

Despite aggregations of turtles on basking sites, basking was a nonsocial activity; groups formed due to the relative shortage of good basking sites.

The little social behavior observed functioned primarily to maintain spacing and allow individuals to position themselves without facing adjacent turtles. A particular orientation (facing the most elevated parts of the log) was favored by most of the turtles. This orientation was consistent among observation periods. Often, if a turtle emerged and turned in the "inappropriate" direction it later turned 180°. Nosing/nudging typically occurred when an animal was blocked from walking forward by a turtle directly in front of it. In virtually all cases the one in front that was nosed/nudged walked forward several steps, often nosing or nudging the one in front of it. This proceeded up the file of basking turtles.

Nosing/nudging is advantageous for turtles emerging from the water or in the middle of a file of basking turtles because it provides space in front. By moving forward, a turtle that has been nosed/nudged avoids having the turtle behind attempt to climb on or over it, possibly dislodging both.

Although basking *Pseudemys nelsoni* at my study site tolerated others touching them, individuals were usually intolerant of others resting on them. They would break contact by moving forward or, if unable to do so, by pushing the other off or swiveling (uncommon). I never saw them stacked as described for other species.

Infrequently a larger individual pushed another with its carapace when attempting to emerge and another was in its path. The initial reaction to this type of pushing was bracing after which the emerging turtle stopped and the turtle that was pushed moved away, space permitting. On one occasion a turtle was toppled when pushed.

Social gaping (threats), snaps, bites or attempted bites were not seen. It is likely that the turtle density was insufficient to evoke the agonistic behaviors reported by others (e.g., Bury et al., 1979; Lovich, 1984).

Nonsocial

Large animals have more difficulty emerging than smaller ones and were more likely to fall off while moving about on a log. Turtles usually swam about the log to locate an area that was clear of baskers or where ascent was easiest. The largest turtles all mounted at the same places on the logs and did not hesitate to push or crawl over smaller turtles basking at these spots. Turtles occasionally emerged on shaded logs.

Kicking typically occurred in bouts. The animal may be responding to an irritation caused by the drying of its appendages. No more than two limbs were kicked simultaneously. Animals usually had their heads withdrawn during kicking, after which they would extend their heads and scan. Kicking, rubbing and moving legs may be different intensities of the same motor pattern. This is the most conspicuous movement performed by basking animals.

When the head was rubbed it was partially withdrawn into the shell. This may by a response to small flying insects such as gnats or mosquitoes as might shaking the head. Other than head rubs, rubbing occurred in bouts with some switching, e.g., rub anterior undersurface of carapace to rub posterior undersurface. The head was usually withdrawn during a bout of rubbing. After the rubbing bout the head was usually extended and the animal scanned.

The slow walk was seen when an animal changed position on a basking site. Nosing the substrate often preceded walking forward. Digit spreading typically accompanied limb extension and was more pronounced with the hindfeet. Usually the digits on both hind feet

were spread simultaneously and slowly. I have not seen limb extension in waterbasking animals.

Behaviors in this category appeared to be largely comfort and repositioning movements, probably due to drying of the integument, as a circulatory aid or related to thermoregulation. Other behaviors involved environmental stimuli; nosing the substrate, scanning and remaining generally alert. Limbs are immediately lowered to the substrate when an animal is disturbed. Animals leaving the log caused most others to extend their heads, scan, or move into the water, most likely due to vibrations set up on the log by the moving turtle.

The optimal basking temperature appeared to be below that encountered on sunlit logs, at least during the summer months. In three cases individually recognizable animals moved into the water then climbed back on within 1 min.

Miscellaneous Behaviors

Rapid retraction occurred under water but air bubbles were not formed suggesting that no hissing sound was produced. Hissing was not always heard by turtles rapidly retracting on land indicating that individuals differed either in their ability or inclination to hiss. Hissing was not audible in animals less than about two years of age. It may function was an antipredator display.

Emotional Behavior

Fearful behavior occurred both in response to my presence and to conspecifics. In the latter case, fearful behavior was observed following approaches, gaping, biting, and other aggressive behaviors.

Out of water fearful behavior was characterized by complete retraction, except when basking. During basking, animals fearful of conspecifics withdrew their head, forefeet and tail, and braced with their hindfeet. This sometimes occurred when one animal approached another, usually smaller individual, from a head-on position. Retraction was observed only by the individual that was approached. On land, complete retraction was the usual reaction to a potential predator (human).

Animals exhibiting anger/annoyance characteristically had their appendages and head extended. This was most commonly observed in the lab, by the recipient of several titillation bouts performed by an insistent conspecific, and in the field, by a male after "first noticing" another male before it initiated an agonistic encounter.

Rubbing the carapace against an object appeared pleasurable. Titillation in juveniles appeared to be pleasurable to the performer, but not recipient, because the performer sometimes continued until the recipient's minor annoyance, indicated by staring at the performer, changed to gapes and snaps.

Animals in the lab became excited when given food. They rapidly associated certain human behaviors with being fed. When these or similar behaviors were performed by humans the animals surfaced or slid off their basking platform and swam toward the person. They then exhibited many individually peculiar behaviors that appeared wholly self-trained. Some swam in circles on the surface with their heads directed upwards. Others would consistently go to the bottom and swim against a corner. These behaviors

are probably best labeled "superstitious" (behavior resulting from and maintained by reinforcements that are independent of the animal's behavior; the animal associating the reinforcement with the behavior it was performing when the reinforcement occurred), produced with operant conditioning by dispensing food to hungry animals independent of their behavior (Skinner, 1948). This vigorous activity diminished once food was proffered.

Juveniles attempting to titillate others vigorously pursued and maneuvered about the recipient. An excited state was also evident in preceding and subsequent behaviors. For example, the performer did not rest between bouts of titillation but briskly swam about the aquarium nosing objects and other individuals.

When an animal was restless it either swam back and forth in the aquarium or against one of the sides. This behavior lasted up to 20 min.

CHAPTER 4

DISCUSSION

Standard Ethograms

Behavioral units

Schleidt et al. (1984) have expressed the need for standard ethograms that would facilitate cross species comparisons and synthetic attempts (see also Schleidt, 1985). A preliminary step would necessitate a consensus on the size of behavioral units and the classes of behavior (i.e., "lumpers" vs. "splitters"). While Schleidt et al. (1984) recognized this problem, they did not provide guidelines; instead they describe how differences of opinion early in the study evaporated with increasing familiarity with their study animal. This approach is representative and appears to satisfy most ethogram architects, however, it does not insure uniformity.

The richness of an animal's repertoire can influence a study in two ways. First, animals with large repertoires will require more time for the researcher to gain familiarity with the species as well as adequately census its behavioral repertoire. Second, animals with smaller repertoires will probably have their behavior scrutinized in somewhat finer detail. This is a direct result of repertoire size (e.g., Wilson, 1976). If two species are compared, one with a small behavioral repertoire and one with a large one, two predictions can be made. First, for the same time invested, the researcher should see a larger proportion of the repertoire, all else being equal (e.g., rates of behavior). Second, on average, each behavior would be seen more often.

Byers and Bekoff (1981), for example, give 147 motor patterns for the collared peccary, *Tayassu tajacu* while Greenberg (1977) gives 76 for the blue spiny lizard, *Sceloporus cyanogenys*. Most would agree that the peccary's repertoire is more than twice as rich as the lizard's. However, data for the latter were obtained in the laboratory under better observation conditions with motor patterns partitioned in finer detail. Such examples suggest that beyond a certain number of motor patterns, acts that would remain separate in behavior-poor repertoires are lumped in behavior-rich repertoires.

The number of categories of behavior listed in an ethogram, while hopefully reflecting the animal's repertoire, is also determined by the observer's ability to recognize patterns (Schleidt et al., 1984) and the degree to which an animal's responses to stimuli are visually or acoustically detectable. Another prominent factor affecting the "graininess" and construction of behavior categories is the orientation of the researcher, e.g., neuroethology or ethological physiology.

Behavior categories and context

Ethologists have long recognized the importance of the criteria by which behaviors are described and classified, since what one records will considerably impact resulting analyses and conclusions. Hinde (1970) recognizes two independent but overlapping approaches: description by form; the strength, degree and patterning of muscular contractions, and description by function; the consequence of a behavior. While he states that there are advantages and disadvantages of both, functional descriptions have attracted more criticism since functions may be obscure or misinterpreted. Purton (1978) pursues this distinction, detailing the philosophical reasons why description by form and by function should remain distinct in the minds of researchers as they observe and record behavior. Drummond

(1981) proposes five dimensions (domains) to objectively define a behavior by form (location, orientation, physical topography, intrinsic properties, and physical effects). In general, researchers consider only a subset of these, possibly leading to misinterpreting behaviors. Errors can be avoided, Drummond (1981) suggests, if the observer is cognizant of which aspects of a behavior are being selectively recorded and which selectively ignored.

Recently, Millikan (in prep; see also Millikan, 1984, 1986, for related discussions) has suggested that the apparent objectivity of description by form is a misconception. She argues that description by form alone has such latitude that only by passing the plethora of motion and changing relations of the animal with its environment through a filter (the observer) can behavior be described. Why are some features of behavior recorded and others ignored? Millikan suggests that we record features that appear to serve a function, we ignore those that do not. Whether the behavior is labeled and described by form or function, she argues that our selective attention is predominantly to functional behaviors. Further, function is restricted to biological function ("proper function"), in brief, historically what the behavior is "used" or "designed" to do (Millikan, 1984). The biological function of a behavior has evolved and is maintained by selection (Millikan, 1984).

In general, the function of a behavior can be experimentally determined (Drummond, 1981), thereby dissipating objections raised by labeling with one scheme rather than another. However, any conspicuous behavior, regardless of its functional importance, is likely to enter an ethologist's catalog. While most conspicuous behaviors may be functionally important, this is not necessarily true, e.g., the function of play is unclear. Another rebuttal to the argument posed by Millikan (above) has been given by Schleidt and coworkers (Schleidt and Crawley, 1980; Schleidt, 1982; Finley et al., 1983). They

propose that the salient features of a behavior's form can be objectively determined if every feature is recorded and the data passed through a rigorous statistical analysis. Features with relatively low variability and consistent association would be retained to describe the behavior. While their studies demonstrate that this approach is theoretically possible for some behaviors, they also document how time consuming such studies are. To construct an entire ethogram using their approach is not presently feasible. Further, it would deal ineffectively with behaviors characterized, in part, by high variability, e.g., much investigatory behavior. One is still left with the question of how behavior is to be classified and described. If by form, how is one to decide which features are important; if by function, how does one treat conspicuous but apparently functionless behaviors?

In practice, behaviors are rarely treated so delicately. Ethologists often concentrate only on a few obvious behaviors, thus avoiding these issues. It is, perhaps, unrealisitic to expect a researcher to devote a large amount of time to meticulously examine every behavior in fine detail. The compromise most ethologists effect is to initially describe the behaviors of interest by their physical form, relying on distinctive characters that best differentiate among them. These definitions (and a better understanding of the behaviors' functions) are refined as observations proceed. Since functions are rarely tested, "presumed function" more accurately reflects actual usage in ethograms. Experimental evidence is sought only in cases where the function is ambiguous or inconsistent with that of related taxa. Ultimately, the purpose of the study, not philosophy, dictates how behavior is classified (see Sherman, 1988). Those who need to know details of behavior patterns use fine units classified by form (e.g., studying behavioral homologies; see Lauder, 1986). Those interested in how the consequences of a behavior affect fitness will develop definitions suggesting presumed function (e.g., Arnold, 1976). As Millikan (in prep.) states, "If there is agreement on anything among current philosophers of science it is

on this: what the data for a given branch of science are and how those data must be described so as to connect with theory are matters adjusted along with theory, and cannot be settled in advance. Theoretical science is, in this respect, always a bootstrapping operation."

Introducing context to a description may inflate subjectivity since it is difficult to demonstrate that the researcher's classification of context matches the animal's. For example, male turtles might treat females differentially based on their likely receptivity, i.e., hormone levels, using olfactory cues. These are cues an observer is unlikely to perceive. With social behaviors, however, context must be included, since many are elicited only by the presence of a conspecific.

Construction of this catalog

In the catalog of the behaviors of *Pseudemys nelsoni*, presented above, I have followed a traditional approach by consulting several of the available ethograms, familiarizing myself with the study animal during reconnaissance observations (Lehner, 1979), and then labeling behavior patterns that were readily identifiable, appeared biologically relevant, and were of sufficient detail to allow presence/absence comparisons with related species without making the catalog unwieldy. In some cases this resulted in unevenness when "lumping" and "splitting", hopefully compensated by making the catalog more useful. Selection of the behavioral units and their graininess was also influenced by a subjective impression of their importance to the subjects.

There are several other attributes a 'standard ethogram' might incorporate, not included in Schleidt et al. (1984). These include some quantification of behavioral frequencies and percent of time occupied by the behavior, the contexts in which specific behaviors are

exhibited (Gordon, 1985), the degree of stereotypy/plasticity in a behavior, and behaviors that are species typical or aid in distinguishing related species. Pictorial representation of the climax state worked well for the blue-breasted quail (Schleidt et al., 1984) and would probably be successful for other (primarily visual) animals. It was useful for depicting some turtle behaviors, primarily static postures, but not others.

Difficulties in Observing Freshwater Turtles

In a study of this nature difficulties arose from two sources; 1) those inherent to the environment in which observations are made, and 2) those specific to the study organism. In (1), the duration and frequency of underwater observation periods were limited. Recording behaviors posed difficulties when attempting to maintain position in a current as inconspicuously as possible. Mobility considerations precluded the use of bulky photographic equipment (e.g., supplementary illumination). Finally, it was necessary to approach the animals quite closely because visibility was limited in areas the turtles frequented. Behaviors recorded in this manner are suspect of bias due to the observer effect (Lehner, 1979).

In (2), problems specific to the study animal, flight distance presented a problem. Some individuals were tolerant of close observation but many more were not. This strongly biased which animal's behaviors were recorded.

In contrast to recording behaviors underwater, observing basking animals posed few problems. Animals were stationary for long periods of time. Social interactions were not frequent and other behaviors appeared to be dictated by environmental conditions or the duration of time the animal was out of water.

Emotional Behavior

Emotion cannot be divorced from motivation (Buck, 1984), thus some (e.g., Fantino, 1973) suggest dropping the term emotion entirely. While this may happen in the future, presently it is more useful for ethologists to retain both terms and allow for overlap between them. Some emotions fit the motivation terminology well, e.g., pleasure, which is believed to accompany many consummatory acts. Nonspecific arousal may comprise several appetitive behaviors since "nonspecific" refers only to my inability to specify arousal states.

Fear has received considerable attention, largely from psychologists, since many fearful behaviors are quantifiable (Suarez and Gallup, 1983). Alarm reactions of turtles to visual stimuli have been quantified and appear similar to those of other taxa (Hayes and Saiff, 1967; Ireland et al., 1969). Fearful responses to predator endotherms should be influenced by temperature since reptiles' reaction time and speed are influenced by it. This was demonstrated for the lizard *Anolis lineatopus* by Rand (1964), although it may not be true for lizards that retreat into secure hiding places when temperatures are below their preferred range (Rand, 1964). While temperature may influence fearful responses to predators, its influence on fearful responses to conspecifics has not been investigated.

In *Pseudemys* turtles, flight distance from predators in the water probably depends on visibility conditions rather than temperature. However, in basking animals many factors are likely involved, even for one class of predators, e.g., humans in a canoe. Casual observations suggested that animals in this study site differentiated classes of canoeists because people fishing could approach basking turtles much closer than those paddling for sport.

Anger and annoyance, likely concomitants of aggressive behavior, have received attention partly because agonistic behavior can be reliably elicited through context manipulation (Jenssen, 1978) or brain stimulation (Vowles and Beasley, 1974). Turtles have not served as subjects in this field. Observations made during this study did not suggest great differences between agonistic behaviors (and presumed accompanying emotions) in *Pseudemys nelsoni* and many other vertebrate taxa. However, the apparent absence of aggressive behavior in *P. floridana* was the single greatest difference between these congeners.

The number of fundamental emotions has been disputed. Most agree that there are at least six in humans (happiness, sadness, anger, fear, surprise, and disgust) from which the others can be derived (Schwartz, 1982). Green and Marler (1979) give ethological activities that correspond to a similar scheme proposed by Plutchik (1970). Some estimates are considerably larger (Izard and Dougherty, 1982, give ten). Others (e.g., Scott, 1980), see some emotions as general while others are taxon specific. Weinrich (1980), unlike those who believe that at least some emotions are general (implying homologous and conservative brain organization), maintains that the number of emotions is not an interesting question. He speculates that the existence of a particular emotion in a taxon relies largely on the adaptive value of the emotion, with phylogeny, size and nervous system complexity acting as obvious constraints. The short list that I give describes only the most obvious emotional behaviors and makes no attempt to be exhaustive.

Frustration is generally not included in shorter lists and may not be a fundamental emotion. However, ethologists should be interested in it because it may underlie the expression of displacement behavior (McCleery, 1983).

I do not consider "surprise/startle" behavior to be emotional behavior. Startle or surprise is the immediate reaction to an unexpected stimulus. If the stimulus is dangerous,

the emotion that follows "surprise" is "fear", making "surprise" a redundant category. If the stimulus is not dangerous, the animal may remain alert, exhibiting the behavior state I label "arousal".

Emotional behavior requires more attention from ethologists, especially with respect to its likely adaptive value.

Issues this Behavioral Catalog can Address

Data similar to these for *Pseudemys nelsoni* and *P. floridana* have not been systematically gathered for other chrysemid (*sensu* McDowell, 1964, hereafter chrysemid) turtles or, for that matter, any semi-aquatic or aquatic chelonian. This makes comparisons difficult or impossible. Still, two questions can be considered: 1) How complete and representative are the results presented here for *P. nelsoni*, and 2) What conclusions can be drawn by comparing the behavior of this turtle with the available data on others?

Habitat Specific Behaviors

The habitat of Rock Springs run may be atypical of *Pseudemys nelsoni*. Typical *P. nelsoni* habitat is usually more eutrophic (Ernst and Barbour, 1972), such as that found in Payne's Prairie. Since underwater observation would be impossible in this type of habitat one is left with the nagging question of whether the behaviors that were observed should be interpreted as 1) best suited to a different habitat, 2) part of a range of variable strategies, individuals using behaviors appropriate for the habitat, or 3) some mixture of the two.

Social behavior appears well adapted for conditions of low visibility. Courtship and many other social encounters seem to be initiated by olfactory cues. Tactile information

may also be important, e.g., during courtship. A female can be readily followed in murky water because the alternating kicks of the hindlimbs intermittently exposes the light striped skin between the hindlimbs and tail, giving the impression of alternating blinking beacons. During my observations, this facilitated following females under dense vegetation mats. Aggressive encounters occurred only when animals were in close proximity. If one animal retreated a short distance, aggressive behavior ceased. There are apparently no long distance social signals. This suggests that these turtles do not take advantage of the water clarity at Rock Springs run but exhibit social behaviors suitable for conditions of poor visibility.

Courtship and Species Discrimination

Jackson and Davis (1972*a*) have suggested that male courtship behavior might serve to identify conspecifics in *Trachemys* and related turtles. This does not appear to be the case for *Pseudemys nelsoni* for reasons discussed below. I do agree with them that titillation by the male serves to slow the female down.

It is unlikely that the titillation display in *Pseudemys nelsoni* alone serves as a species isolating mechanism. Courtship of *P. nelsoni* is very similar to that of *P. concinna* (Jackson and Davis, 1972*b*) and *P. floridana* (personal observations). Like many animals, the female indicates her willingness only at the end of a protracted courtship. This may increase her sons' fitness by endowing them with a persuasive suitor's genes (Fisher, 1958). For the male, who must follow the female for a considerable distance and time, courtship is time-consuming and appears energetically expensive. Courtship by male *Trachemys scripta* has also been described as energetically costly (Jackson and Davis,

1972*a*). This should select for males who court only suitable females, i.e., conspecific females.

The duration of the titillation bout appears much more variable in *Pseudemys nelsoni* (620 msec ± 340 SD, $n = 9$)(Kramer and Fritz, 1989) than *P. concinna* (506 msec ± 22.2 SD, $n = 10$?)(Jackson and Davis, 1972*b*) or *T. scripta* (808 msec ± 12.12 SD, $n = 9$?)(Jackson and Davis, 1972*a*). These estimates may be unrepresentative since sample sizes were small (Kramer and Fritz, 1989, measured only one male). These data and my observations of *P. floridana peninsularis* courting suggest that too much variation and overlap exist for titillation to serve as the only means of species identification.

In courtship, there appear to be two times when a species discrimination could be made. The first occurs when the male investigates the female. His decision to initiate courtship to a female probably depends on species specific olfactory cues. The second occurs when the female decides to accept or reject the male. Assuming she is receptive, her decision may be based on the male's courtship performance. A female *P. nelsoni* need only infrequently make a species discrimination in nature. Except for the mix-up described above, no male was ever seen trailing or courting a female of the wrong species in the field.

Comparison with Other Turtles

There is some data available for a comparison of aquatic social behaviors, compiled by Carpenter and Ferguson (1977). Using their categories, I compared the social behavior of *Pseudemys nelsoni* from this study with behaviors observed in other chrysemid turtles (Tables 3 and 4).

Using the behavior categories listed by Carpenter and Ferguson (1977), *Pseudemys nelsoni* has 50-60 social behaviors, only slightly more than the 50 given for *Terrapene*

carolina (Carpenter and Ferguson, 1977). This suggests that an upper limit for the number of social behaviors possessed by a single species of turtle may have been approached. Sadly, only 37 different behaviors have been reported for all other species of chrysemid turtles combined, reflecting how poorly known the social behaviors of these genera are. This makes comparisons difficult since the absence of a behavior from the literature does not reliably signify its absence from the species.

In many taxa, dominance hierarchies are established by intensive fighting. Later, to reinforce dominance relationships, brief agonistic encounters, unlikely to lead to injury ("squabbling"), may occur (McBride, 1964). Male-male interactions of *Pseudemys nelsoni* are probably best labeled as "squabbling", functioning to maintain a dominance hierarchy (Kramer, 1986). However, not only did *P. floridana* not exhibit agonistic behavior but, compared to *P. nelsoni*, males infrequently approached and interacted with conspecific males. Thus, fundamental differences may exist between the social structures of *P. nelsoni* and *P. floridana*. In the lab, juvenile *P. concinna* exhibited more intraspecific aggression then did juvenile *P. nelsoni* or *P. floridana*. An investigation of their social structure would probably be rewarding.

The nonsocial aquatic behaviors of other turtles have not been reviewed and are so sketchily reported that comparisons with this catalog are not yet warranted. Ernst and Barbour (1972) give perhaps the most detailed general descriptions of North American turtles. Moll and Legler (1970) discuss some behaviors of a Central American *Trachemys*. Nonsocial aquatic behaviors may differ little among closely related species. At this study site, only trivial differences were noted between the nonsocial aquatic behaviors of *Pseudemys nelsoni* and *P. floridana*.

Despite the inadequacies of the behavioral data on chrysemid turtles, some points can be made. First, there is extensive behavioral overlap among the species. This is not

unexpected when considering phylogeny, morphology, and gross habitat preferences. The greatest divergence appears among courtship behaviors of the *Trachemys* complex (Jackson and Davis, 1972*a*; Davis and Jackson, 1973; Moll and Legler, 1970). The effect of this, if any, on reproductive isolation has not yet been examined. Other behavioral differences are largely due to the presence/absence of a small class of behaviors. Second, lists of this sort are not useful in distinguishing among possible social systems. As one example, the same agonistic behaviors may be common to both hierarchical and territorial social systems. Lists of behaviors and their definitions when used to compare different species need to be supplemented by contextual and frequency information. Third, considerably more research is needed to address comparative ethological questions on chrysemid turtles. Behavior catalogs of species related to *Pseudemys nelsoni* need to be completed and placed in a framework that reveals the relationship between social systems and habitat and to delineate individual strategies within their social context.

LITERATURE CITED

Ainley, D. G. 1974. The comfort behavior of Adelie and other penguins. Behaviour 50, 16-51.

Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49, 227-267.

Arnold, S. J. 1976. Sexual behaviour, sexual interference and sexual defense in salamanders, *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. Z. Tierpsychol. 42, 247-300.

Auth, D. L. 1975. Behavioral ecology of basking in the yellow- bellied turtle, *Chrysemys scripta scripta* (Schoepff). Bull. Florida State Mus. Biol. Sci. 20, 1-45.

Belkin, D. A. and C. Gans. 1968. An unusual chelonian feeding niche. Ecology 49, 768-769.

Bjorndal, K. A. 1986. Effect of solitary vs. group feeding on intake in *Pseudemys nelsoni*. Copeia 1986, 234-235.

Boice, R. 1970. Competitive feeding behaviors in captive *Terrapene carolina*. Anim. Behav. 18, 703-710.

Buck, R. 1984. The communication of emotion. Guilford Press, N.Y. 391 pp.

Burghardt, G. M. 1985. Animal awareness: Current perceptions and historical perspective. Amer. Psychol. 40, 905-919.

Bury, R. B. 1979. Population ecology of freshwater turtles. *In* Harless, M. and H. Morlock (Eds.), Turtles: Perspectives and Research. John Wiley & Sons, N.Y. Pp. 571-602.

Bury, R. B., J. H. Wolfheim and R. A. Luckenbach. 1979. Agonistic behavior in free-living painted turtles (*Chrysemys picta bellii*). Biol. Behav. 1979, 227-239.

Byers, J. A. and M. Bekoff. 1981. Social, spacing and cooperative behavior of the collared peccary, *Tayassu tajacu*. J. Mammol. 62, 767-785.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 1939, 170-173.

Cagle, F. R. 1955. Courtship behavior in juvenile turtles. Copeia 1955, 307.

Carpenter, C. C. and G. W. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles. *In* Gans, C. (Ed.), Biology of the Reptilia, Vol. 7. Academic Press, N.Y. Pp. 335-554.

Chance, M. R. A. 1962. An interpretation of some agonistic postures: The role of "cut-off" acts and postures. Symp. Zool. Soc. London 8, 71-89.

Darwin, C. 1965. The Expression of Emotions in Man and Animals. Univ. of Chicago Press, Chicago. 372 pp.

Davis, J. D. and C. G. Jackson, Jr. 1973. Notes on the courtship of a captive male *Chrysemys scripta taylori*. Herpetologica 29, 62-64.

Drummond, H. 1981. The nature and description of behavior patterns. *In* Bateson, P.P.G. and P.H. Klopfer (Eds.), Perspectives in Ethology, vol 4: Advantages of diversity. Plenum Press, N.Y. Pp. 1-33.

Ernst, C. H. and R. W. Barbour. 1972. Turtles of the United States. Univ. of Kentucky Press. 347 pp.

Exline, R. V. 1982. Gaze behavior in infants and children: a tool for the study of emotions? *In* Izard, C. E. (Ed.), Measuring Emotions in Infants and Children. Cambridge Univ. Press, N.Y. Pp. 164-177.

Fagen, R. M. and R. N. Goldman. 1977. Behavioural catalogue analysis methods. Anim. Behav. 25, 261-274.

Fantino, E. Emotion. *In* Nevin, J. A. and G. S. Reynolds (Eds.), The Study of Behavior: Learning, Motivation, Emotion, and Instinct. Pp. 280-320.

Finley, J., D. Ireton, W.M. Schleidt, and T.A. Thompson. 1983. A new look at the features of mallard courtship displays. Anim. Behav. 31, 348-354.

Fisher, R. A. 1958. The genetical theory of natural selection, 2nd Ed. Dover, N.Y. 291 pp.

Gordon, D.M. 1985. Do we need more ethograms? Z. Tierpsychol. 68, 340-342.

Green, S. and P. Marler. 1979. The analysis of animals communication. *In* Marler, P. and J. G. Vandenbergh (Eds.), Handbook of Behavioral Neurobiology, Vol. 3. Plenum Press, N.Y. Pp. 73-158.

Greenberg, N. 1977. An ethogram of the blue spiny lizard, *Sceloporus cyanogenys* (Reptilia, Lacertilia, Iguanidae). J. Herpertol. 11, 177-195.

Hayes, W. N. and E. I. Saiff. 1967. Visual alarm reactions in turtles. Anim. Behav. 15, 102-106.

Hinde, R.A. 1970. Animal behaviour: a synthesis of ethology and comparative psychology, 2nd ed. McGraw-Hill, N.Y. 876 pp.

Hinde, R. A. 1985. Was 'The Expression of the Emotions' a misleading phrase? Anim. Behav. 33, 985-992.

Ireland, L. C., W. N. Hayes and L. H. Laddin. 1969. Relation between frequency and amplitude of visual alarm reactions in *Pseudemys scripta*. Anim. Behav. 17, 386-388.

Izard, C. E. 1982. Introduction. *In* .Izard, C. E. (Ed.), Measuring Emotions in Infants and Children. Cambridge Univ. Press, N.Y. Pp. 3-18.

Izard, C. E. and L. M. Dougherty. 1982. Two complementary systems for measuring facial expressions in infants and children. *In* Izard, C. E. (Ed.), Measuring Emotions in Infants and Children. Cambridge Univ. Press, N.Y. Pp. 97-126.

Jackson, C. G., Jr. 1977. Courtship observations on *Chrysemys nelsoni* (Reptilia, Testudines, Testudinidae). J. Herpetol. 11, 221-222.

Jackson, C. G., Jr. and J. D. Davis. 1972*a*. A quantitative study of the courtship display of the red-eared turtle, *Chrysemys scripta elegans* (Wied). Herpetologica 28, 58-64.

Jackson, C. G., Jr. and J. D. Davis. 1972*b*. Courtship display behavior of *Chrysemys concinna suwanniensis*. Copeia 1972, 385-387.

Jackson, D. 1978. *Chrysemys nelsoni* (Carr). Florida red-bellied turtle. Cat. Amer. Amphibians and Reptiles 210, 1-2.

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia Univ. Press, N.Y.

Jenssen, T. A. 1978. Display diversity in anoline lizards and problems of interpretation. *In* Greenberg, N. and P. D. MacLean (Eds.), Behavior and Neurology of Lizards: An Interdisciplinary Colloquim. NIMH, Rockville, Maryland. Pp. 269-285.

Jordan, R. H. and G. M. Burghardt. 1986. Employing an ethogram to detect reactivity of black bears (*Ursus americanus*) to the presence of humans. Ethology 73, 89-115.

Kramer, M. 1986. Field studies on a freshwater Florida turtle, *Pseudemys nelsoni*. *In* Drickamer, L. C. (Ed.), Behavioral ecology and population biology. Privat, I.E.C., Toulouse. Pp. 29-34.

Kramer, M. and U. Fritz. 1989. Courtship of the turtle, *Pseudemys nelsoni*. J. Herpetol. In press.

Lardie, R. L. 1973. Notes on courtship, eggs, and young of the Florida red-bellied turtle, *Chrysemys nelsoni*. Hiss News-Journal 1, 183-184.

Lardie, R. L. 1983. Aggressive interactions among melanistic males of the red-eared slider, *Pseudemys scripta elegans* (Wied). Bull. Oklahoma Herpetol. Soc. 8, 105-117.

Lauder, G. V. 1986. Homology, analogy, and the evolution of behavior. *In* Nitecki, M. H. and J. A. Kitchell (Eds.), Evolution of animal behavior: Paleontological and field approaches. Oxford Univ. Press, N.Y. Pp. 9-40.

Legler, J. M. 1956. A social relation between snapping and painted turtles. Trans. Kansas Acad. Science 59, 461-462.

Lehner, P. N. 1979. Handbook of Ethological Methods. Garland STPM Press, N.Y. 403 pp.

Lewis, M. and L. Michalson. 1982. The measurement of emotional state. *In* Izard, C. E. (Ed.), Measuring Emotions in Infants and Children. Cambridge Univ. Press, N.Y. Pp. 178-207.

Litwin, S. 1975. Basking Activity in the Eastern Painted Turtle, *Chrysemys picta picta.* M.S. Thesis, Rutgers University. 54 pp.

Lovich, J. E. 1984. An Analysis of Aggressive Basking Behavior in the Eastern Painted Turtle. M.S. Thesis, George Mason University. 79 pp.

McBride, G. 1964. A general theory of social organization and behaviour. Univ. of Queensland Fac. Papers Vet. Sci. 1, 75-110.

McCleery, R. H. 1983. Interactions between activities. *In* Halliday, T. R. and P. J. B. Slater (Eds.), Animal Behaviour, Vol 1: Causes and Effects. W. H. Freeman and Co., N.Y. Pp. 134-167.

McDowell, S. B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London 143, 239-279.

Marchand, L. J. 1944. Notes on the courtship of a Florida terrapin. Copeia 1944, 191-192.

Marchand, L. J. 1945. The individual range of some Florida turtles. Copeia 1945, 75-77.

Millikan, R. G. 1984. Language, thought, and other biological categories. Bradford Books/MIT Press, Cambridge, Mass. 355 pp.

Millikan, R. G. 1986. Thoughts without laws; cognitive science with content. Phil. Rev. 95, 47-80.

Millikan, R. G. (*in prep*) What is behavior? or why narrow psychology/ethology is impossible. *To appear in* Red queen psychology and other essays for Alice. Bradford Books/MIT Press, Cambridge, Mass.

Moll, E. O. and J. M. Legler. 1971. The life history of a neotropical slider, *Pseudemys scripta* (Schoepff), in Panama. Bull. Los Angeles Co. Mus. Nat. Hist. 11, 1-102.

Moynihan, M. H. 1970. Control, suppression, decay, disappearance, and replacement of displays. J. Theor. Biol. 29, 85-112.

Phillips, R. R. 1977. Behavioral field study of the Hawaiian rockskipper, *Istiblennius zebra* (Teleostei, Blenniidae). I. Ethogram. Z. Tierpsychol. 43, 1-22.

Plutchik, R. 1970. Emotions, evolution and adaptive processes. *In* Arnold, M. B. (Ed.), Feelings and Emotions. Academic Press, N.Y. Pp. 3-24.

Plutchik, R. 1980. A general psychoevolutionary theory of emotion. *In* Plutchik, R. and H. Kellerman (Eds.), Emotion: Theory, Research, and Experience, Vol. 1. Theories of Emotion. Academic Press, N.Y. Pp. 3-33.

Pritchard, P. C. H. and W. F. Greenhood. 1968. The sun and the turtle. Int. Turtle and Tortoise Soc. J. Jan.-Feb. 1968, 20-25, 34.

Purton, A. C. 1978. Ethological categories of behaviour and some consequences of their conflation. Anim. Behav. 26, 653-670.

Rand, A. S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45, 863-864.

Rand, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc. U.S. National Museum 122, 1-79.

Rundquist, E. M. 1985. *Pseudemys scripta elegans* (red-eared slider) behavior. Herp. Review 16, 113.

Schleidt, W.M. 1982. Stereotyped feature variables are essential constituents of behavior patterns. Behaviour 72, 230-238.

Schleidt, W.M. 1985. In defense of standard ethograms. Z. Tierpsychol. 68, 343-345.

Schleidt, W.M. and J.N. Crawley. 1980. Patterns in the behaviour of organisms. J. Social Biol. Struct. 3, 1-15.

Schleidt, W. M., G. Yakalis, M. Donnelly and J. McGarry. 1984. A proposal for a standard ethogram, exemplified by an ethogram of the bluebreasted quail (*Coturnix chinensis*). Z. Tierpsychol. 64, 193-220.

Schwartz, G. E. 1982. Psychophysiological patterning and emotion revisited: a systems perspective. *In* Izard, C. E. (Ed.), Measuring Emotions in Infants and Children. Cambridge Univ. Press, N.Y. Pp. 67-93.

Scott, J. P. 1980. The function of emotions in behavioral systems. *In* Plutchik, R. and H. Kellerman (Eds.), Emotion: Theory, Research, and Experience, Vol. 1. Theories of Emotion. Academic Press, N.Y. Pp. 35-56.

Sherman, P.W. 1988. The levels of analysis. Anim. Behav. 36, 616-619.

Skinner, B. F. 1948. "Superstition" in the pigeon. J. Exp. Psychol. 38, 168-172.

Suarez, S. D. and G. G. Gallup, Jr. 1983. Emotionality and fear in birds: A selected review and reinterpretation. Bird Behav. 5, 22- 30.

Sugerman, R. A. and R. A. Hacker. 1980. Observer effects on collared lizards. J. Herpetol. 14, 188-190.

Taylor, E. H. 1933. Observations on the courtship of turtles. Univ. of Kansas Science Bull. 21, 269-271.

Vowles, D. M. and L. D. Beasley. 1974. The neural substrate of emotional behavior in birds. *In* Goodman, I. J. and M. W. Schein (Eds.), Birds: Brain and Behavior. Academic Press, N.Y. Pp. 221-258.

Walker, W. F., Jr. 1979. Locomotion. *In* Harless, M. and H. Morlock (Eds.), Turtles: Perspectives and Research. John Wiley and Sons, N.Y. Pp. 435-454.

Ward, J. P. 1984. Relationship of Chrysemyd Turtles of North America (Testudines: Emydidae). Special publications of the Museum of Texas Tech. Univ., Texas Tech Press, Lubbock, Texas. 50 pp.

Weinrich, J. D. 1980. Toward a sociobiological theory of emotions. *In* Plutchik, R. and H. Kellerman (Eds.), Emotion: Theory, Research, and Experience, Vol. 1. Theories of Emotion. Academic Press, N.Y. Pp. 113-138.

Wilson, E. O. 1976. A social ethogram of the neotropical arboreal ant *Zacryptfocerus varians* (Fr. Smith). Anim. Behav. 24, 354-363.

Zipko, S. J. 1982. The basking behavior of painted turtles. Amer. Biol. Teacher 44, 406-412.

APPENDIX 1

TABLES AND FIGURES

Table 1. Field dates and hours of observation at the Apopka, Fla. field site.

Date	Hours of Observation	
	Underwater	Basking
Sept. 10 - 20, 1983	4.6	-
Dec. 13 - 30, 1983	14.3	11.4
Apr. 22 - May 19, 1984	30.4	7.4
June 15 - July 1, 1984	16.4	-
Aug. 27 - Sept. 20, 1984	46.2	5.8
May 20 - June 18, 1985	36.9	18.8

Table 2. ANOVA testing the effects of sex, time of day, and their interaction on the proportion of time *Pseudemys nelsoni* turtles were observed.

Source of Variation	df	Mean Square	F-ratio	p
Sex	1	0.00769	0.672	0.44
Time Period	3	0.01237	0.360	0.78
Sex by Time Period	3	0.01939	1.694	0.24
Error	8	0.01144		

Note: Time of day was divided into morning (< 1100), noon (1100 - 1400), afternoon (1400 - 1700) and evening (> 1700). No effects were significant.

Table 3. Behaviors seen in *P. nelsoni* in this study and listed in Carpenter and Ferguson (1977), relating primarily to intraspecific aggression, courtship and mating.

number	description	reported in other chrysemid turtles
1	extend head	x
2	retract head into shell	x
3	raise head high while neck extended	
4	lower head while neck extended (olfactory)	x
8	tilt or tip head	
9	strike or lunge (rapidly)	
10	nudge with head	x
11	sniff with snout, head to head	x
13	crook head by inclining (arching) [= 4?]	x
16	pulsate throat	x
17	bite, nip or snap	x
18	grasp, drag with jaws	x
19	gape with mouth	x
21	open eyes	
22	close eyes	x
27	extend legs from shell	x
28	retract legs into shell	x
29	raise or lift up legs	
30	lower legs	
31	swing legs	x
34	wipe with foot or leg	
37	foot	
38	close foot	
39	rotate foot	x
44	raise tail, bring tail up	
45	lower tail, bring tail down	x
46	retract tail	
47	straighten tail [= extend tail?]	x
48	curl or bend tail	x
57	push with shell (using legs)	x
62	tilt shell laterally	
64	pivot shell [= 76]	x
68	swimming (forward)	x
69	swimming (backward)	x
70	swim in a circle or semicircle	x
72	sink to bottom in water	x
73	walk forward	
76	pivot [= 64]	x
77	lunge forward	
79	face same direction, head to head	
80	face one another, anterior presentation [= 11?]	x

Table 3. (continued)

number	description	reported in other chrysemid turtles
81	lateral presentation	
82	positioned one above the other	x
83	perpendicular arrangement of shells	
84	occupy alert position, all appendages extended	
85	emit sound (hiss)	x
86	void (defecate)	x

Note: The number given is from the list of Carpenter and Ferguson (1977). The last column indicates its presence in other chrysemid (*sensu* McDowell, 1964) turtles (from Carpenter and Ferguson, 1977).

Table 4. Behaviors not seen in this study in *Pseudemys nelsoni* but seen in other chrysemid (*sensu* McDowell, 1964) turtles, as listed by Carpenter and Ferguson (1977).

Number	Description
6	swing head from side to side (olfactory)(*T. scripta*)
23	spray, boil from nostrils (*T. grayi* and *T. ornata*)
32	flex legs, clasp or pinion with legs (*P. floridana*)
35	bring legs together in bilateral adduction (*P floridana, T. scripta*)
40	clasp with feet, hook with nails, flex toes (*C. picta, T. scripta*)
42	caress, stroke, scratch, click with nails (*P. concinna, T. grayi, T. ornata, T. scripta, C. picta*)
49	twist, turn with torque, rotate tail (*P. floridana*)
5	entwine tails (2 individuals)(*T. scripta*)

Note: Numbers and behavioral descriptions follow Carpenter and Ferguson (1977). Species that exhibit these behaviors are in parentheses.

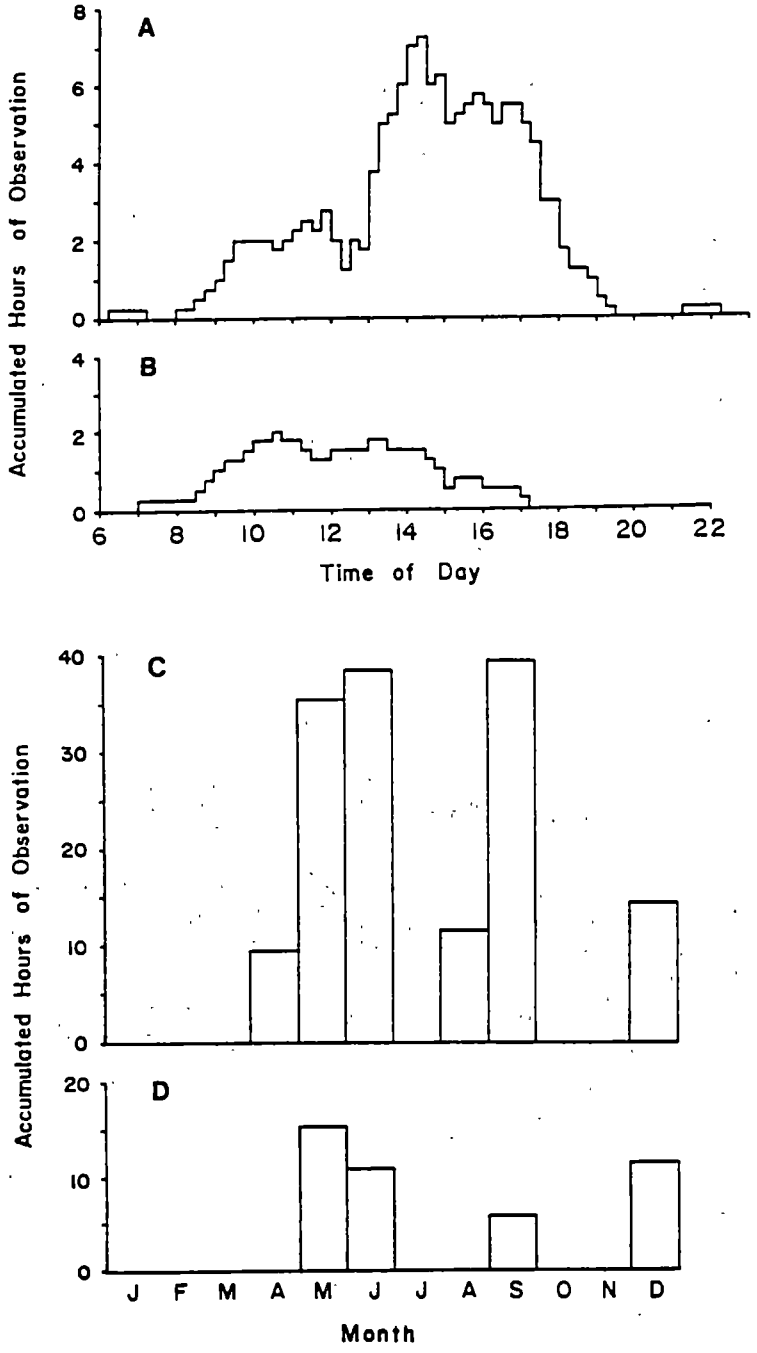

Figure 1. Hours of field observations. A. Distribution of underwater observations by time of day in 15 min blocks, corrected to eastern standard time. B. Distribution of basking observations by time of day in 15 min blocks, corrected to eastern standard time. C. Distribution of hours of underwater observations by month of year. D. Distribution of hours of basking observations by month of year.

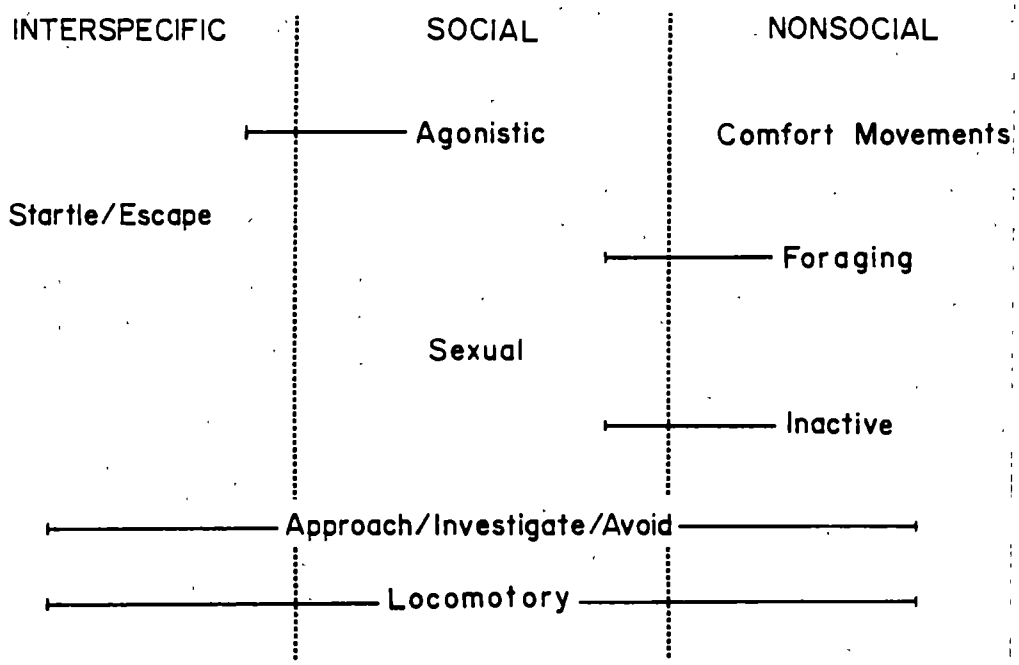

Figure 2. General relationship between context (interspecific, social and nonsocial) and functional categories in the aquatic behaviors of *Pseudemys nelsoni*. Bars indicate functional categories in more than one context.

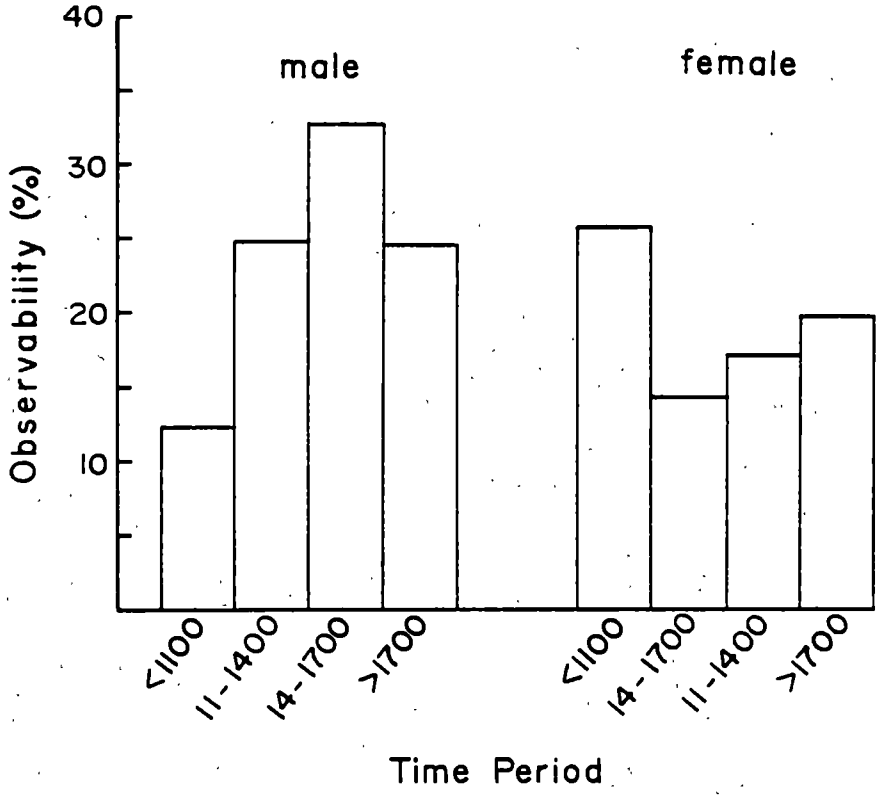

Figure 3. Percent of time in each of four time periods that male (left) and female (right) *Pseudemys nelsoni* were observed while making underwater observations. For each sex and time period combination the durations of all animals on which data were taken were summed and then divided by the total amount of time spent underwater for that time period. This gives an index of how "observable" males and females were throughout the day.

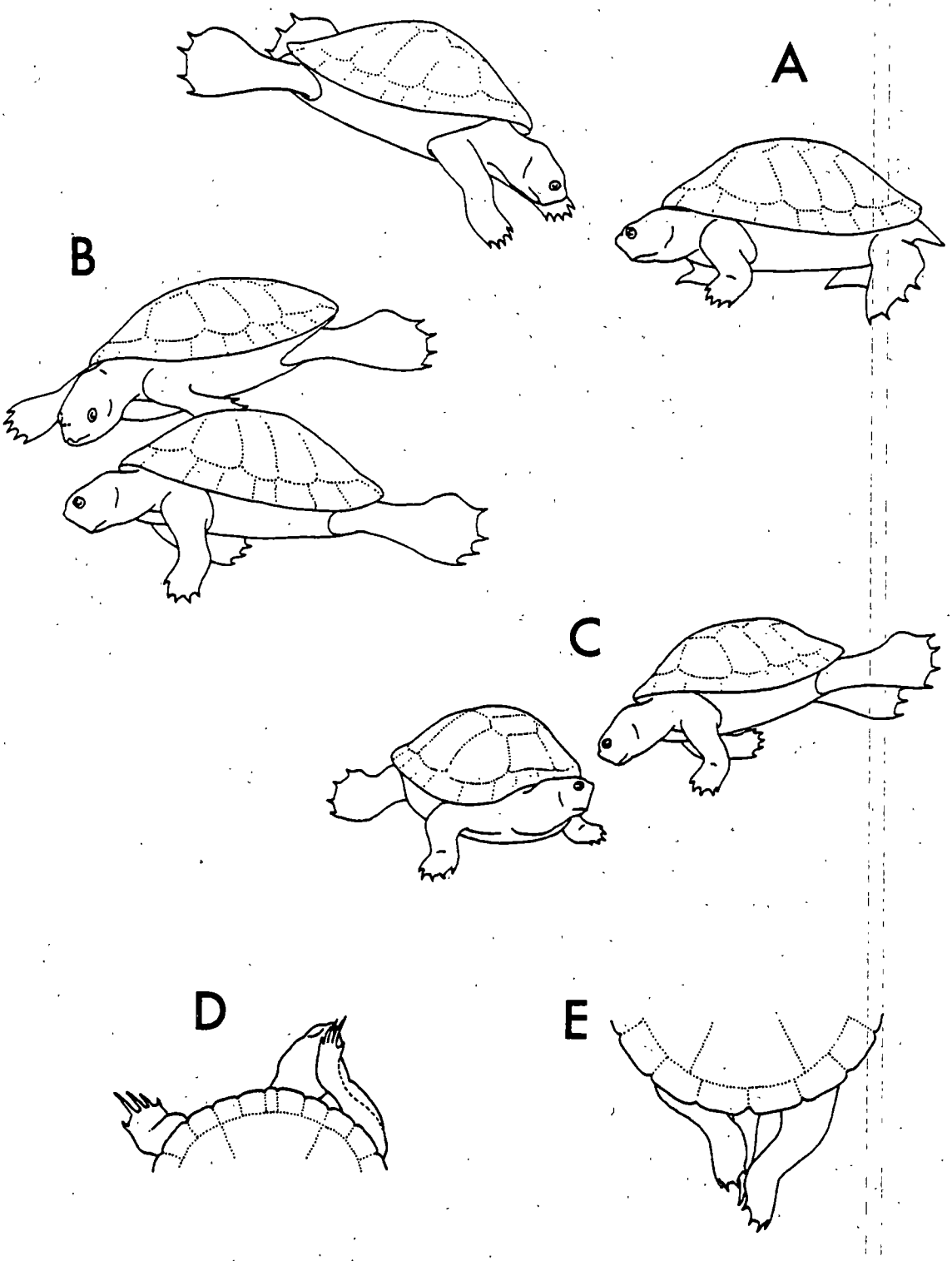

Figure 4. Approaches of one juvenile *Pseudemys nelsoni* to another in the water and rubbing. A. Head on, B. From behind, and C. From the side. D. Head rubs. E. Rubbing the two hindfeet and tail together.

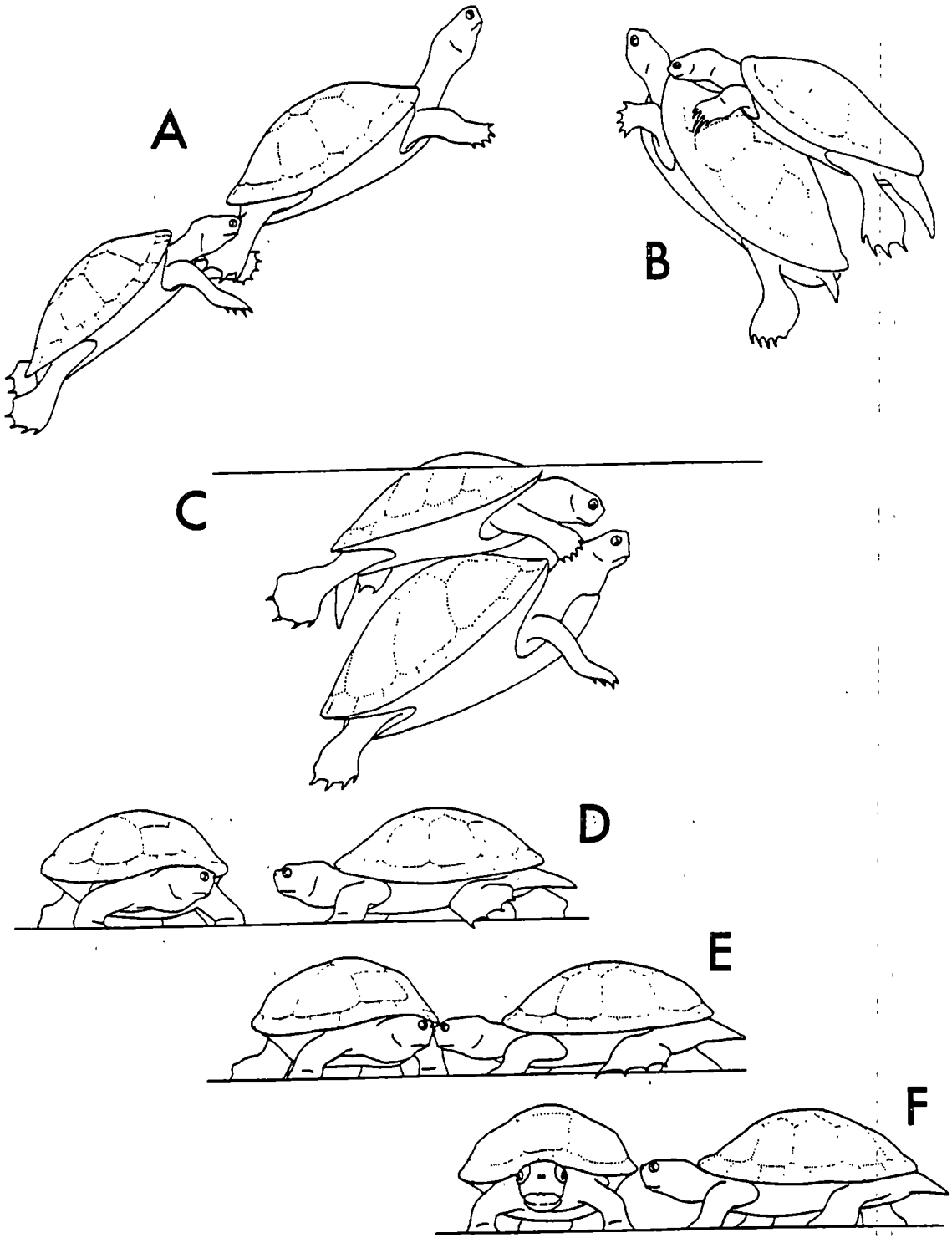

Figure 5. Investigatory postures. Nosing by A. An adult male of an adult female *Pseudemys nelsoni*, B. By an adult male *P. floridana* of an adult female *P. nelsoni*. C. Approach of a male to a female *P. nelsoni* prior to a bout of titillation. D - F. Sequence of postures of two juvenile *P. nelsoni* during nosetouching.

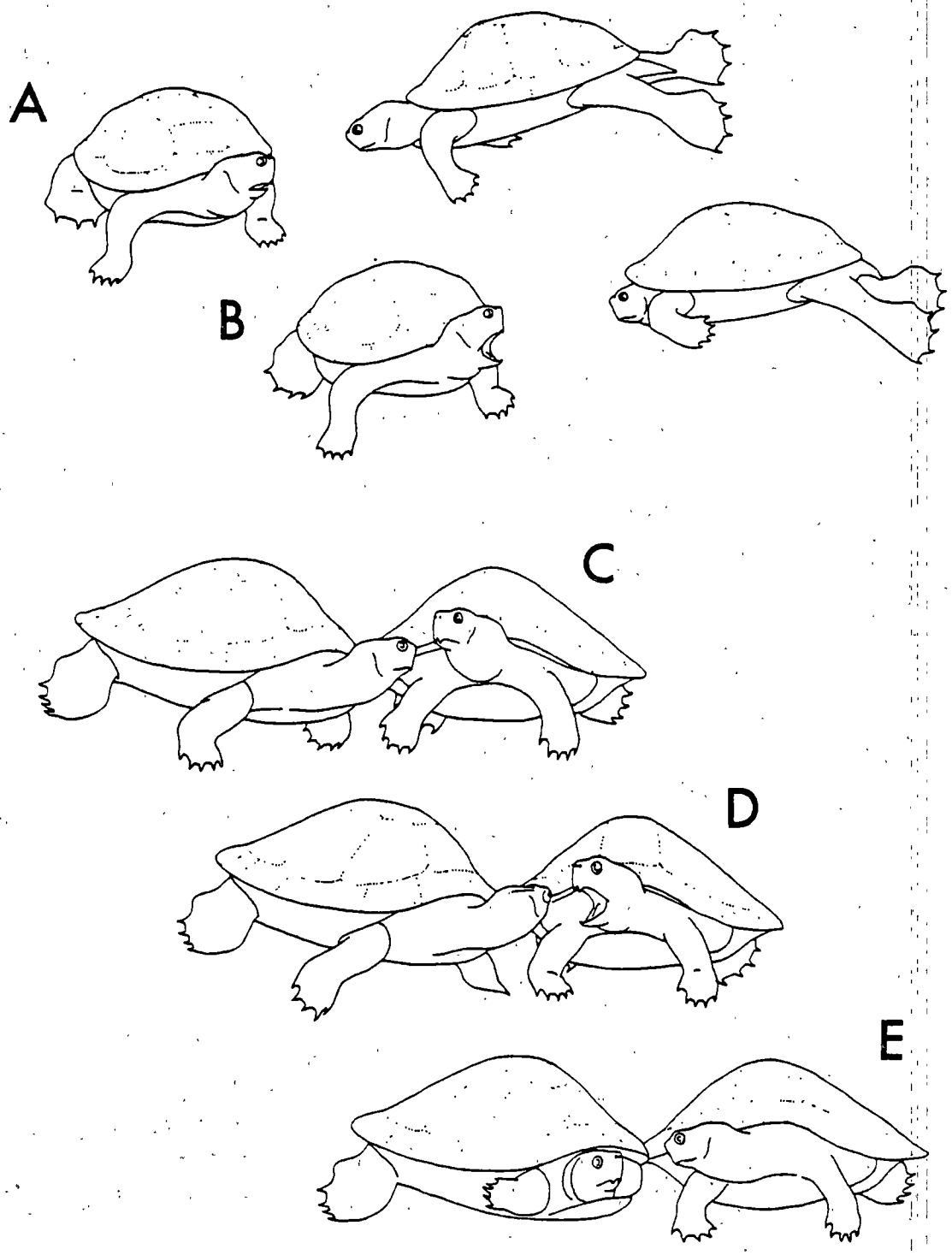

Figure 6. Social postures (1). A, B. Sequence of postures by two juvenile *Pseudemys nelsoni* when the left individual gaped at one approaching from the right. C - E. Sequence of postures by two juvenile *P. nelsoni* during a snap by the individual on the right.

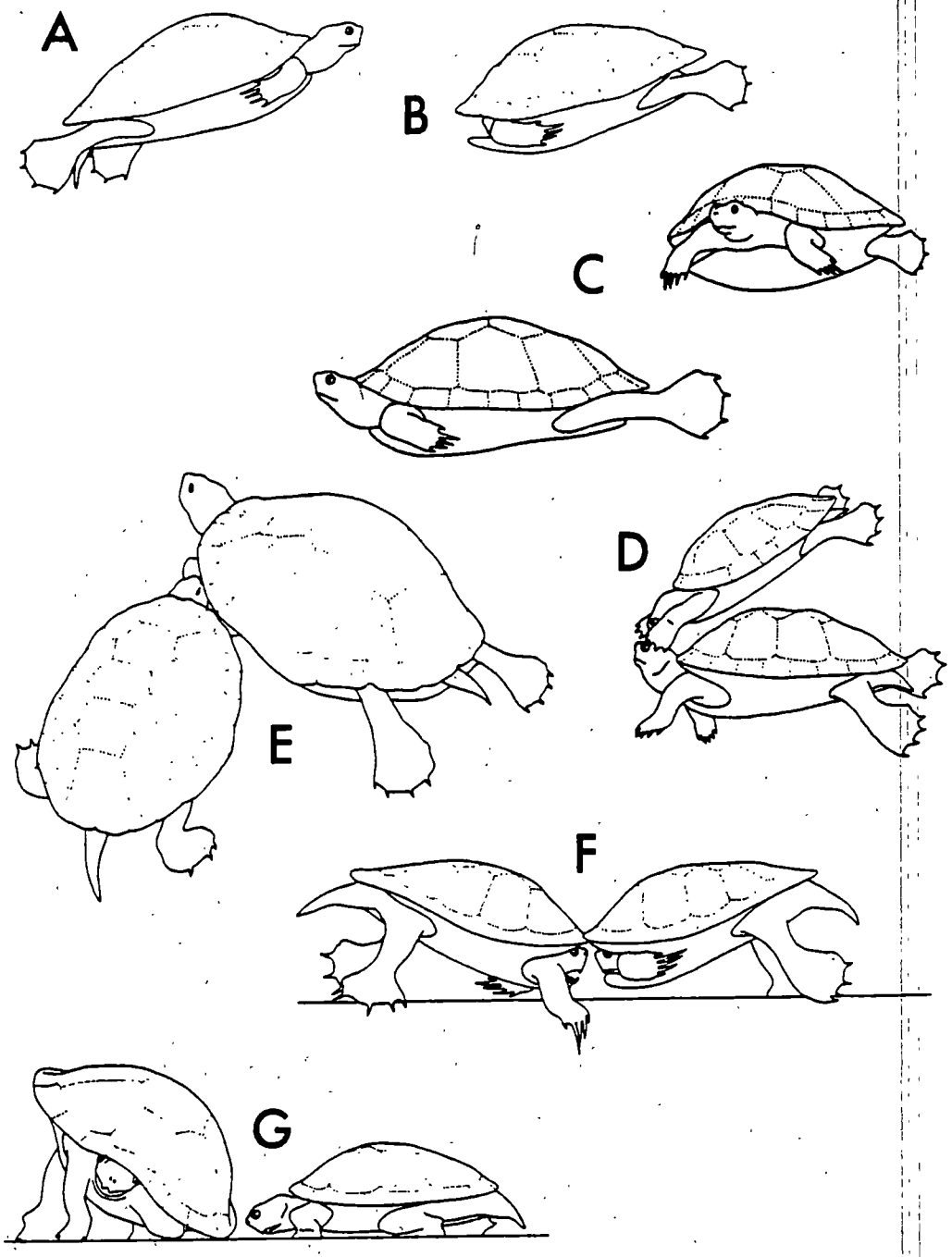

Figure 7. Social postures (2). Postures of two male *Pseudemys nelsoni* during an agonistic interaction: A. "Dominant" posture by winning male. B. "Subordinate" posture of losing male. C. Male *P. nelsoni* on right chasing another. D. Precocial courtship in *P. nelsoni* depicting the swim above position. E. Male *P. nelsoni* biting left forelimb of female *P. nelsoni* during an agonistic encounter. F. Pushing by two male *P. nelsoni* on substrate during an agonistic encounter. G. Female *P. nelsoni* tilts body in response to an approaching male.

APPENDIX 2

FREQUENCIES AND PERCENTS OF BEHAVIORS

Observed occurrences (freq.) and percent of total duration of individual behaviors and behavior categories of *Pseudemys nelsoni* and *P. floridana* recorded in the field. Categories and numbers correspond to those given in the text. The total number of recorded behaviors and their summed duration are given in the text.

	Pseudemys nelsoni				*Pseudemys floridana*				
	male		female		male		female		
Behavior	freq.	%	freq.	%	freq.	%	freq.	%	Notes
I. AQUATIC BEHAVIORS									
Foraging	22	6.5	29	16.0	4	3.4	9	1.0	includes moving between sites
Approach/Investigate/Avoid	163	6.2	63	3.5	80	7.6	69	3.2	
1. Approach	26	<1.0	3	<1.0	20	2.4	4	<1.0	opposite sex conspecific
	29	1.0	2	<1.0	5	<1.0	8	<1.0	approach and/or nose same sex conspecific
	11	<1.0	0	0.0	3	<1.0	0	0.0	approach and/or nose opposite sex heterospecific
	0	0.0	2	<1.0	3	<1.0	0	0.0	approach and/or nose same sex heterospecific
	86	3.9	46	2.8	47	4.1	53	2.6	approach, investigate observer
2. Follow	3		0		1		0		to same sex conspecific
	1		0		1		0		to same sex heterospecific, see also Swim above
3. Nose	0		8		0		2		substrate or objects only
4. Turn toward (orient to)	7		2		0		2		conspecifics
Comfort Movements	6		12		1		1		
2. Rubbing/ scratching	5		5		0		1		
3. Yawning	1		7		1		0		
Locomotory	446	32.4	269	24	115	18.7	258	20.4	
1. Swimming	422	31.2	248	23.0	111	18.4	247	18.3	
5. Walk	23	1.1	20	<1.0	4	<1.0	9	<1.0	
6. Burrowing	1	<1.0	1	<1.0	0	0.0	2	1.6	

	Pseudemys nelsoni				*Pseudemys floridana*				
	male		female		male		female		
Behavior	freq.	%	freq.	%	freq.	%	freq.	%	Notes
Agonistic	92	4.2	47	5.2	2?	0.0	3?	0.0	(individual acts)
Male-male aggressive behavior	34	3.5	NA	NA	0	0.0	NA	NA	
4. Gape	14		0		0		0		to same sex conspecific
	0		1		0		0		to opposite sex conspecific
6. Social and attempted social bites	13		0		0		0		nudge/bite/snap or attempted bite to same sex conspecific
	2		1		2?		1?		bite/attempted bite to opposite sex conspecific
7. Withdrawal of head and front limbs	13	1.0	1	<1.0	0	0.0	0	0.0	retract head during interaction
11. Complete retraction	0		1		0		1		
12. Retreat	5		2		0		1		
13. Chase	3		0		0		0		same sex conspecific
	2		0		0		0		opposite sex conspecific
14. Push	2		0		0		0		to same sex conspecific
	1		0		0		0		to opposite sex conspecific
15. Drag	1		1		0		0		
16. Circle	3		0		0		0		
17. Lateral presentation	0		3		0		0		to approaching or near opposite sex conspecific
18. Tilt body	0		2		0		0		
19. Kicks	0		2		0		0		to opposite sex conspecific
20. Grip	8	2.9	8	4.5	0	0.0	0	0.0	male grips female's forelimb with mouth
21. Yanking	8	<1.0	8	<1.0	0	0.0	0	0.0	number of interactions with yanking, male gripping female's forelimb
22. Clattering	17		17		0		0		number of bouts
Sexual	39	1.6	20	2.5	14	13.8	11	8.0	
1. Swim above	19	1.6	19	2.5	11	13.8	11	8.0	Swim above and male following female
3. Titillation	19		0		3		0		number of bouts
4. Mounting (transition to copulation)	1		1		0		0		

	Pseudemys nelsoni				*Pseudemys floridana*				
	male		female		male		female		
Behavior	freq.	%	freq.	%	freq.	%	freq.	%	Notes
Miscellaneous maintenance behaviors									
3. Defecation	1		2		0		0		
Inactive	282	44.8	182	48.3	67	56.3	151	67.3	
1. Rest	238	41.1	132	40.6	45	42.1	105	51.9	at surface
	36	3.1	48	7.6	20	13.9	44	15.3	on bottom, cannot reach surface
3. Resting on others on bottom	6	<1.0	0	0.0	2	<1.0	2	<1.0	
4. Waterbasking	2		0		0		0		during underwater observation only
5. Rest in substrate	0	0.0	2	<1.0	0	0.0	0	0.0	
II. BASKING BEHAVIORS									
Social	19		11		1		3		
1. Nose/nudge	2		1		0		0		
2. Climb/rest on another	11		3		0		0		
3. Touches	2		2		1		1		
4. Push off	1		1		0		0		
5. Swivel	1		0		0		0		
6. Push with shell	1		2		0		2		
7. Bracing	1		2		0		0		
Nonsocial	796		360		45		60		
1. Emerge from the water	116		32		6		17		successful
	2		0		2		2		not successful (6 others not identified to species and/or sex)
2. Into water	103		34		6		8		
3. Turning in position	45		17		13		9		
4. Kicking	67		53		1		2		number of bouts, also includes some rubbing movements
5. Moves legs	45		13		1		1		

	Pseudemys nelsoni				*Pseudemys floridana*				
	male		female		male		female		
Behavior	freq.	%	freq.	%	freq.	%	freq.	%	Notes
6. Rubbing	37		14		0		1		rubs head
	1		0		0		0		rubs appendage against substrate
	1		0		0		0		rubs above tail
7. Appendage retraction and extension	127		72		4		8		extends or retracts head or appendages
8. Raises/lowers appendage	32		46		2		9		
9. Raises/lowers head	102		31		3		0		
10. Shake head	3		1		0		0		
11. Scan	12		7		2		0		
12. Walking	95		30		5		3		
14. Nose substrate	6		10		0		0		
16. Yawn	2		0		0		0		

PART 3

PATTERNS OF BEHAVIOR IN JUVENILE *PSEUDEMYS NELSONI*

CHAPTER 1

INTRODUCTION

Predicting what an animal will do based on its recent behavior has long interested ethologists, whether to reduce long streams of behavior into manageable summaries or to uncover the empirical "rules" that animals use to assemble units of behavior (Dawkins and Dawkins, 1973, 1976; Crane, 1978). Behavior sequences of individual animals can be analyzed in two basic ways. One is time based, where durations of behaviors and the time intervals between them are examined statistically or modeled (e.g., Metz, 1974; Delius, 1969, Andersson, 1974; van der Kloot, 1975; Heiligenberg, 1973). Fagen and Young (1978) give a detailed treatment of temporal behavior analysis. The second way ignores time and instead looks for patterns in the sequence of behaviors; which behaviors are most likely to precede or follow a given behavior.

To look for patterns in the sequence of behaviors one typically starts by constructing a transition matrix from the sequences of behaviors and then testing to see if a first order Markov chain (Crane, 1978), where the likelihood of a behavior occurring depends only on the previous behavior, is a more appropriate model than a "random" model, based only on total behavior frequencies. If sufficient data exist, higher order Markov chains can be explored. Transition matrices can also be made from lagged transitions (Douglas and Tweed, 1979). Here, if a first order Markov chain does not adequately explain the data, one tests if a transition matrix to second following behaviors is adequate, etc. Another possibility is to cluster behaviors into subunits, each subunit composed of several linked behaviors (Fentress and Stilwell, 1973). The two latter alternatives circumvent the difficulty of collecting sufficient data for higher order Markov chain analysis. Additional

techniques to analyze behavior sequences have been developed from information theory, e.g., one can calculate the increase in predictability, or reduction in uncertainty, by knowing one or more previous behaviors (Chatfield, 1973). Sequential behavior analysis assembles behaviors related by position; some authors have used these techniques to suggest a hierarchical structure to behavior (e.g., Dawkins and Dawkins, 1973; Fentress and Stilwell, 1973). Examples of extracting patterns from behavior sequences of birds are Lemon and Chatfield (1971) and Slater and Ollason (1972); flies, Dawkins and Dawkins (1976); lizards, Cooper (1977, 1979); and ants, Douglas and Tweed (1979). Bekoff (1977) and Fagen and Young (1978) give general discussions of this approach.

Predictability increases when behavior units are more molecular (finely divided)(Cane, 1978), exemplified by the many detailed analyses of one category of behavior; e.g., grooming behavior in blowflies (Dawkins and Dawkins, 1976), singing in cardinals (Lemon and Chatfield, 1971), and courtship in the fish, *Corynopoma riisei* (Nelson, 1965 [in Metz, 1974]). Another situation with high predictability occurs when the attainment of a goal consists of a short sequence of relatively stereotyped behaviors, e.g., adult frogs capturing prey (Biedermann, 1988).

When behavioral units are far apart in time, predictability may be good if the behaviors can be mapped onto day length, tide or some other aspect of the environment with strong Zeitgebers. However, in these cases, only gross (molar) behavior categories can be reliably predicted. Some predictability of finer behavior units is possible because they occur with a certain probability within the larger categories. For example, swallowing is more likely to occur during foraging than during sleeping.

It is the behaviors and time units in between that pose the greatest prediction problems. This may be due to both looser relationships among behavior categories and constraints of the human nervous system to process the information (Dawkins, 1983), frequently

requiring statistics to identify the "rules". The focus of this investigation was twofold; to explore relationships among the behaviors of juvenile turtles in this time framework, and to evaluate the differenct approaches to unraveling streams of behavior.

CHAPTER 2

MATERIALS AND METHODS

Sequences of behavior on four three-year old *Pseudemys nelsoni* turtles were collected in the laboratory using focal animal sampling (Altmann, 1974) and checksheets (Fig. 1). The subjects were hatched from eggs laid by two captive females and subsequently maintained in a polystyrene container measuring 122 x 70 x 48 cm for 3 years, then transferred to a 180 x 39 x 33 cm aquarium in which observations were made. In addition to the juvenile *P. nelsoni*, two juvenile *P. concinna suwanniensis* and three juvenile *P. floridana peninsularis* shared the aquarium.

Behaviors in 30 s intervals were ordered by marking their occurrence with a number rather than a check (Hinde, 1970). Data were collected in 20 to 60 min observation periods in the early afternoon, one or two hours after feeding. At this time animals were in the water and likely to be active. The focal animal was determined randomly, thus total observation times for each animal are unequal (Table 1). Individuals were not pooled due to problems of independence (Machlis et al., 1985), since inhomogeneous samples, if treated as homogeneous, are likely to produce falsely significant test results (Metz, 1974).

Behavior categories used were exhaustive and mutually exclusive, definitions are given below:

1. **surface:** swimming vertically or diagonally to the surface for breathing; resting or swimming at the surface with the head out of water.
2. **swim:** all swimming in a horizontal plane above the substrate, not including swimming at the surface or during **interact (init)**.

3. **crawl**: locomotion on the substrate, if not included in **eat**, **to bottom**, or **interact (init)**.

4. **to bottom**: mostly vertical movement, by swimming, crawling (rare) or sinking, to reach the substrate.

5. **still**: subject not engaged in one of the other activities, no locomotion for 5 - 10 s.

6. **eat**: ingesting food, includes crawling if for short distances and swimming if eating from the surface.

7. **interact (init)**: subject approaches another turtle within one body length and investigates it or attempts to initiate an interaction (e.g., aggression, precocial courtship).

8. **interact (recip)**: subject is approached within one body length by another turtle who investigates it or attempts to initiate an interaction with the subject. A response by the subject may not occur although ongoing behavior (e.g., **eating**) is usually interrupted.

The data were analyzed in several ways to provide, when collated, a better understanding of the "rules" governing behavior (e.g., van Rhijn, 1977). Approaches such as spectral analysis (Delius, 1969; see Metz, 1974, for others) were not feasible because behavior durations were not recorded. The approaches used in this study were: 1) first order Markov chains, 2) lag sequential analysis, 3) information theory, 4) stationary distribution of behaviors, 5) "natural" behavior units, and 6) behavior associations in time. These are explained in more detail below. Briefly, (1) fitting a first order Markov chain allows one to locate significant positive or negative transitions among pairs of behaviors. This is extended with (2), lag sequential analysis, which locates significant positive or negative transitions of two behaviors separated by one or more behaviors. The use of information theory (3) permits one to assess the increase in predictability (or reduction in

uncertainty) by knowing the previous behavior and to estimate the length of Markov chain necessary to adequately describe the sequences. (4) By calculating the stationary distribution of behaviors, one can determine whether the data are stationary (a prerequisite for many of the other analyses). If the sampled and stationary distribution differ, diurnal cycles may be indicated. "Natural" behavior units (5) are repeated units of three or more behavior occurring commonly in behavior sequences. An analysis of associations in time (6) identified behaviors that were found to be positively or negatively associated with others when separated by various time durations. The first five are sequence based analyses and the last time based.

Sequence Based Analyses

Transition Matrices

The sequences were transcribed to remove contiguous repetitions of the same behavior. First order Markov models for each turtle were constructed using the technique described by Bishop, et al. (1975). The purpose of this analysis was to identify significant transitions, where one behavior was significantly more or less likely than chance to follow another.

Alternation between two behaviors, termed trills by Dawkins (1976), appears to be characteristic of many species, from blowflies (Dawkins and Dawkins, 1976) to cardinal singing (Lemon and Chatfield, 1971). It was considered important enough by Douglas and Tweed (1979) to have devoted considerable effort to removing the overwhelming effect that long sequences of trills have on teasing apart relationships of the other behaviors. I did not remove trills in this study. This is partly because it complicates an analysis by augmenting

the number of behavior categories (and consequently lowering expected cell frequencies) and partly because trills were not as common in the samples of behavior analyzed in this study as they were in the samples of ant behavior analyzed by Douglas and Tweed (1979).

The transition frequencies between pairs of behaviors were calculated for each turtle by a Pascal program (all Pascal programs were written by the author) and the resulting matrices, with structural zeroes along the diagonal, analyzed using Hiloglinear in SPSS-X to locate significant transitions. Transitions were considered significant if the χ^2 standardized residual $(x_i - m_i) / m_i^{1/2}$, where x_i is the observed and m_i the expected cell frequency, exceeded 1.96 or was less than -1.96. These approximate plus or minus one standard normal deviate. Other methods exist to examine internal cells for significance but, as pointed out by Bishop, et al. (1975), the correct method is to remove the cell in question using a structural zero and retest the matrix. One can then evaluate the cell based on the difference between the two G values, with one df. This amount of recomputation would have been unrealistic for the number of matrices and questionable cells in this study.

The transition matrices were then reanalyzed after transforming off diagonal cells with small expected frequencies to structural zeroes. The Pascal program was subsequently modified to yield lagged transition matrices. For lag 1, all adjacent behavior triplets were used to fill the transition matrix with the middle behavior ignored. All behaviors except the first and last two of an observation period were therefore included in three different triplets. This strategy was continued with quartets (with the two middle behaviors ignored), quintets, etc. until lag 10 matrices were calculated. The purpose of this analysis was twofold; to extend the first order Markov chain by examining transitions among pairs of behaviors that were separated by one or more behaviors, and to examine interindividual differences by locating transitions among behavior pairs that differed among turtles.

G-tests were made on individual matrices to test for independence of prior and subsequent behaviors. Cells with low expected frequencies were eliminated to make G-tests valid. G-tests were also made among matrices to test for differences among turtles, using a C_{13}, C_{23} configuration (Bishop et al., 1975) (turtle = 1, prior behavior = 2, subsequent behavior = 3). Deviant cells were identified using χ^2 deviates. Significant first order transitions, discussed above, differ slightly from the lag 0 matrices since cells with low frequencies were not eliminated in the former. This is a result of different objectives, the former was to identify transitions that were probably important, the latter to obtain valid G-tests.

Markov Chains and Stationarity

Markov chains are often used by ethologists to summarize data, probably due to the ease of calculation and interpretation; however, the assumption of stationarity, necessary for valid G-tests and information theory statistics, is unlikely to be met by behavioral data (Slater, 1973). If the data are stationary, transition probabilities do not change with time. Behavior A would be just as likely to be followed by behavior B at the beginning of the observation period as at the middle or end. However, even in the absence of variable external stimuli, an animal's internal state changes with time, which may be expressed as changing transition probabilities. This is one reason that the assumption of stationarity is likely to be violated.

Another potential source of nonstationarity is due to interactions with other turtles because transition probabilities are likely to change during interactions and as a result of them (Oden, 1977). Since the most recent introductions to the aquarium were several months prior to this study and all *P. nelsoni* subjects had been kept for several years,

interactive behavior among the animals should be stable among observation periods. Similar reasoning underlies Heiligenberg's (1973) procedure of keeping juvenile *Tilapia maria* with each focal *Haplochromis burtoni* cichlid.

Although no in-depth analysis of violating the assumption of stationarity is available in the behavioral literature, there were two reasons for believing that it might not be a serious problem for these data. First, if changes in transition probabilities (internal state) occurred infrequently during the observation period, the transition matrix would appear more random than were the actual data. This is because important transitions occurring in only one part of the observation period would be "diluted" by those same behaviors occurring randomly elsewhere in the observation period. Unfortunately, the converse, that unimportant transitions may appear falsely significant, is still problematic for the same reason that pooling individuals in not advised. The second reason justifying the use of Markov chains is that if one takes data at the same time each day, as in this study, the changes in transition probabilities should fluctuate about a mean, with the effects of daily cycles removed (Slater, 1973; Crane, 1978).

To investigate the assumption of stationarity, matrices of transition frequencies for sequential 20 min portions of each observation period were created. Unfortunately, expected cell frequencies were so low as to preclude meaningful G-tests among the matrices. As an alternative, 10 min sliding sums were calculated by taking 10 min sums every 2.5 or 5 min. Results for some of the longer observation periods are given in Figure 2. In some observation periods the proportions of the eight behaviors changed rapidly and erratically with time, e.g., T1-11/14 and T4-11/17, while in others they changed little, e.g., T4A-11/22. These results suggest that the assumption of stationarity is violated, at least for some observation periods. Haccou, et al. (1983) have developed a technique to determine

when the transition probabilities change but their method requires continuous time based data.

An additional assumption of Markov chains is that the animal has a finite memory (Crane, 1978), presumably within the order that will be analyzed using Markov chains. However, we know that the memory, defined psychologically, of many animals extends for weeks or months, depending on the subject to be recalled. Even short term memory probably exceeds the length of time used in most sequence analyses. Memory, in the broad sense that applies to Markov chains, is also good, hence the high predictability of daily cycles. A further limitation of Markov chain analysis that it is unlikely to identify bouts and clusters of bouts. Bout analysis (e.g., Machlis, 1977) would be more useful in revealing these patterns.

In summary, Markov chain analysis ignores longer processes (cycles) and transition rules not dependent solely on the previous few behaviors. Thus, behavior is usually more structured than a Markov chain analysis will reveal.

Other Sequential Techniques

Information theory techniques as applied to behavior sequences were used to estimate reductions in uncertainty by knowing the previous behavior and to estimate the order of Markov chain necessary to explain the data satisfactorily (the average number of previous behaviors useful in predicting the current behavior). The calculations were programmed, directly following the methodology given by Chatfield (1973) and Steinberg (1977).

The stationary distribution of behaviors for each turtle was calculated by projection using a Pascal program. The stationary behavior distributions are analogous to stable age distributions, giving the same kind of information, projected proportion of each behavior if

transition frequencies do not change. These are compared to the proportions of each of the behaviors for the four turtles. If there are differences between the sampled and stationary distributions, the data may not be stationary. Nonstationarity detected by this method could be due to diurnal cycles, e.g., if there was a tendancy for animals to rest more often towards the end of observation periods, the stationary distribution would have a larger proportion of **still** than the sampled one.

Fentress and Stilwell (1973) have suggested that streams of behavior be analyzed by looking for sequences of behaviors that form natural units, i.e., behaviors that are usually only associated with certain other behaviors, often in a particular order. A Pascal program counted all identical strings of 3-9 behaviors for all observation periods of each turtle and listed the most common ones.

Time Based Analyses

To examine the relationships of the behaviors in time, the original data sheets were transcribed into a file giving the number of times each behavior occurred in each sequential 30 s interval. This file differed slightly from that described above since repeated behaviors were not removed. The object of this analysis was to identify behaviors that occurred more or less frequently than chance when separated by various time intervals from other behaviors. For example, if surfacing (to breathe) occurred regularly, say about once every other minute, one would expect surface to be positively associated with itself in intervals encompassing multiples of 120 s. A separate analysis was performed for each observation period.

A Pascal program was used to calculate the associations among behaviors for seven time intervals and perform G-tests (goodness-of-fit) on all associations in each time interval

excluding cells with an expected frequency of less than five. The intervals used were: (1) behaviors that occurred within 60 s of each other, (2) behaviors that occurred between 60 and 150 s of each other, (3) between 150 and 300 s, (4) between 300 and 450 s, (5) between 450 and 600 s, (6) between 600 and 750 s, and (7) between 750 and 900 s. The 0 - 150 s interval was separated into (1) and (2) to distinguish significant associations as close in time as possible without creating too many cells with low expected frequencies. For the same reason, the two possible cross-associations (behavior A preceding B vs. B preceding A) were not separated.

Expected frequencies for each time interval were constructed as follows. First, the proportion of each behavior in the observation period was calculated. Next, the total number of associations in that time interval was calculated. Finally, the sum was multiplied by the proportions of the two behaviors of that association. Freeman-Tukey cell deviates (Bishop, et al., 1975) were used to locate significant positive or negative associations, again using a $\pm$ 1.96 cutoff. Significant associations were classified into one of three groups corresponding to a p of 0.05, 0.01 and 0.001 ($\pm$ 1.96, $\pm$ 2.58 and $\pm$ 3.32). The program was run on eight of the longer observation periods, two per turtle.

CHAPTER 3

RESULTS

First Order Markov Chains

In this section I first present a traditional first order Markov chain approach, then use these results as a reference from which the results of other types of analyses may be compared. For example, if one behavior is positively linked to a second and the second to a third, a greater than expected frequency of the first to third is likely with a lag of one (that is, with one behavior intervening between the two). Similarly, positively linked behaviors should be closely associated in time.

Significant positive and negative first order transitions and summaries for the four turtles are given in Figure 3. The difference in the number of significant transitions in Turtles 3 (few) or 4 (many) versus Turtles 1 and 2 is due largely to sample size. Frequencies of these transitions are depicted by the first bar of each histogram panel in Figures 4-11.

Rather than examine all significant first order linkages, which would be tedious to read and of little general interest, I comment only on those that were found in at least three of the four turtles (Fig. 3) with the hope that these linkages are characteristic of *Pseudemys nelsoni* at this age and perhaps of related species.

Behaviors 1 and 2, **surface** and **swim** were positively linked in all turtles, although when retesting the transition matrices by putting structural zeros in cells with low expected frequencies, some of the chi-square deviates shrunk to slightly below the ± 1.96 cutoff. From Figures. 4 and 5 one sees that **surface** and **swim** tend to alternate. This pattern is

strongest in Turtle 1, its positive cell deviates are often significantly greater than those of the three other turtles in the panels **swim** to **swim**, **swim** to **surface**, and **surface** to **swim** (Figs. 4 and 5).

Since these two behaviors tend to alternate, one expects them to be closely associated in time. Figure 12 gives associations in detail for one observation period of one turtle to aid in interpreting Figures. 13 and 14, which give associations for eight observation periods illustrating deviates from expected frequencies. In half of the observation periods **swim** and **surface** were more likely to be found together than expected in the same 60 s interval. This linkage was also evident when the streams of behavior were subjected to a search for repeated units of 3 - 9 behaviors (Table 2). One explanation for the linkage of these behaviors is that swimming is an energetic behavior, requiring frequent breathing.

In three of four turtles, **swim** was linked with **to bottom** in a first order Markov chain. At other even lags, **to bottom** also tended to follow **swim** due to the **surface-swim** alternating pattern. **Swim** and **to bottom** were also found more frequently than expected within 60 s of each other in six of eight observation periods (Fig. 13).

To bottom was followed by **eat** significantly more often than chance in three of four turtles. The sequence **swim, to bottom, eat** was common in two turtles (Table 2). **Eat** was, in turn, followed by **interact (recip)** more often than chance, that is, animals that were eating were proportionally more likely be become engaged in interactions initiated by others than when they were performing other behaviors. **Interact (recip)** was also likely to be followed by **eat**; after the interaction the animal resumed eating. A tendency for these behaviors to alternate with each other can be seen in the sixth and eighth rows of panels in Figures 9 and 11. Repeated units of **eat** and **interact (recip)** were found in two turtles (Table 2).

There are four first order sequences that occurred significantly less often than expected. In all turtles **swim** was unlikely to be followed by **eat**, and in three of the four **eat** was unlikely to be followed by **swim**. **Swim** was unlikely to be followed by **eat** since **to bottom** usually interceded between the two if animals ate food on the substrate. Occasionally, animals ate food from the surface, in which case **swim**, **surface** and **eat** occurred in the same 30 s interval on the checksheet. Thus, the low frequencies of the **swim-eat** transitions are most likely due to food location and not the animals.

The transition of **swim** to **interact (recip)** was unlikely in all turtles; that is, a swimming turtle was unlikely to be engaged in an interaction by another while swimming. Since most interactions consisted of precocial courtship sequences, this differs markedly from adults, where males only court moving females (Kramer and Fritz, 1989). These two behaviors also tended not to occur in the same 60 s interval in half of the observation periods for which data were sufficient for G-tests (Fig. 13).

Finally, **to bottom** to **surface** was an uncommon transition in three of the four turtles. This did not appear as a negative association within 60 s intervals suggesting that animals arriving on the substrate usually perform one or more behaviors before surfacing.

Having established that there are several significant positive and negative first order transitions, one next asks how useful that is in predicting behavior sequences. In other words, how much uncertainty about which behavior will appear next in a behavior stream is removed by knowing the previous behavior?

Information theory provides us with an estimate of this, the normalized transmission (Steinberg, 1977). The percent reductions in uncertainty, corrected with the closed form approximation (Steinberg, 1977) are: Turtle 1, 25.6%; Turtle 2, 26.2%; Turtle 3, 32.0%; Turtle 4, 26.9%. Thus, on average, there is a moderate increase in predictability by knowing the previous behavior and the subjects do not differ greatly in this respect.

How much additional uncertainty would be reduced by knowing additional previous behaviors? While data limitations precluded G-tests on higher order Markov chains, information theory provides a technique to estimate the order of dependency (Chatfield, 1973). Graphs of unconditional uncertainty were constructed for each of the four turtles (Fig. 15). An "elbow" in a graph corresponds to a large drop in the average uncertainty if the order is incremented by one. A clear "elbow" does not appear in any graph. The largest drop, at least in Turtles 3 and 4, is associated with a first order chain although subsequent drops are also sizable. These drops were not tested for significance because the test statistic that would be used, $2(\log_e 2)N_{i+1}T_i$, is the same as the likelihood ratio test statistic (Chatfield, 1973) and both would be invalid due to the large number of cells with very low expected frequencies. However, the graphs suggest that minimally a fourth or fifth order Markov chain would be necessary to adequately describe these streams of behavior. This is reinforced by re-examining Table 2 and noting the large number of repeated "units" of four or more behaviors, mostly repeated pairs of behaviors.

The proportions of behaviors differ little from the stationary distribution of behaviors (Table 3). This is probably a result of sampling several observation periods per animal and combining the transition frequencies. However, this also suggests that a tendency to move from one internal state to a second was not consistent over observation periods (Fig. 2), i.e., there was no influence of diurnal cycles during observation periods.

Short Term Cycles

Another characteristic exhibited by some streams of behavior is cyclicity. While the effects of daily cycles were hopefully eliminated through scheduled sampling, short term cycles, on the order of minutes, could exist. Below I examine the evidence for cycles,

when two behaviors tends to be separated by regular time intervals or, in a behavior sequence, occupy the same position in relation to one another. These relationships are usually not amenable to a Markov chain analysis because very large data sets are required to examine higher order chains. Two approaches will be discussed; lag sequential analysis and auto- and cross-associations (Andersson, 1974).

In lagged sequences (Figs. 4 - 11), the most common pattern of significant cells is alternate high and low frequencies between behavior pairs. To avoid presenting redundant information, only the frequencies of following behaviors are presented, say A following B (B to lagged A). To visualize the lagged frequencies of A preceding B, one need only to reverse the panel of behavior A to lagged B. The lagged frequencies of a behavior preceding itself is a mirror image of the behavior following itself, with zeroes at the immediately preceding and following cells (lag 0).

The alternation of high and low frequencies between behavior pairs is partially due to the behavior definitions. If I had included the behavior 'pause', there would have likely been some repeated triplet patterns. Panels with significant cells involving larger lags but not smaller ones were rare (Figs. 4 - 11), indicating that the 4th or 5th order Markov chains that would be necessary to describe the behavior sequences are largely an artifact of repeated behavior pairs. Differences among turtles were quantitative rather than qualitative. For example, Turtle 1 showed a stronger **surface-swim** pattern than other turtles. The one exception was the response of Turtle 2, the only male, to interactions initiated by other turtles. It usually crawled away, often followed by another approaching it. Turtles 1, 2 and 4 usually did not react as strongly when other animals initiated interactions. In any case, similarities among the turtles' behavior patterns are more striking than differences. I suspect that some of the difference among turtles may be attributed to sampling since there was great variation among observation periods of a single turtle.

Overall G-test results on the matrices are given in Table 4. In Turtles 2 - 4 there is a trend for the matrices of larger lags to have a larger p (the model of independence of prior and subsequent behaviors is a better fit). There is not a similar trend for differences among turtles. Except for lag 0, differences in transition frequencies among turtles were roughly the same across all lags examined. These differences are related to the strength of behavior patterning among the turtles. At lag 0, the difference among turtles was much greater, suggesting not only that it is inappropriate to pool individuals but that interindividual differences in sequences of behavior are more pronounced for transitions of immediately adjacent behavior pairs.

Below I discuss associations in time (Figs. 13 - 14). In these data there were many significant cells but patterns common to all eight observation periods were rare. Some of the trends not previously discussed are given below.

The **swim-to bottom** association was greater than expected in six of eight observation periods in the within 60 s time interval, also seen in first order Markov chains. The **swim-still** association occurred significantly less than expected in three of six observation periods in the <60 and 60 - 150 s time intervals, suggesting a short term active-inactive cycle. Supporting this, in two observation periods **still** was positively associated with itself when close in time but negatively when further. Significant associations of **still** and other behaviors tended to be negative (T3-11/16, T4-11/17) especially with **interact (recip)**. Of all associations with the latter behavior in which significant cells could be examined, 51% were negative, 18% positive, and 31% neither. This suggests that when animals are **still** they are ignored by others.

CHAPTER 4

CONCLUSIONS

When observing these turtles their behavior, at the level addressed in this study, does not appear highly organized. One reason for this may be the constraint of the way humans extract patterns on certain time scales (Dawkins, 1983). Certainly the sequence of the component acts of each behavior used here would be strongly linked (Crane, 1978), the reason that the behaviors can be easily and relatively unambiguously defined. Another reason that organization may not be evident at this time scale is that it may be weak, at variance with these results. Strong patterns within observation periods are evident but, with a few exceptions, they are not common to all observation periods. This inconsistency may be one reason that, without statistical assistance, it is difficult to extract the organization of behavior at this level.

Evidence has been presented demonstrating temporal cycles of various lengths. Finer behavior units would have no doubt yielded additional shorter cycles, longer observation periods, longer cycles. For single observers longer continuous observation periods are methodologically unsound because accuracy greatly diminishes with increased observation time (Altmann, 1974). In retrospect, an additional behavior, pause, would have been useful since animals sometimes hesitated for a few s before exhibiting one of the coded behavior patterns. This would have allowed some behaviors, such as **eat**, to be examined in more detail without overly taxing data collection.

Some of the "rules" that have been extracted from the behavior of turtles in this study can be compared with what one would a priori predict. For example, surfacing and energetic behaviors should be coupled. This was the case for frequencies of **surface** and

swim in this study and **surface** and precocial courtship in Part 5. Eating and initiating interactions with others usually belong to different motivational systems in animals and it is not surprising that they tend not to be temporally adjacent here.

Since several methods were used to analyze these data, one naturally asks which were the most useful. All give somewhat different information, so this may be unfair. Nevertheless, I found my adaptation of Fentress and Stilwell's (1973) method of finding natural behavior units to give a reasonably clear picture of how behavior sequences are assembled but not to indicate the strength of patterning. Lag sequential analysis was difficult to interpret. A first order Markov approach would probably be most useful following identification of natural behavior units followed by a graph of unconditional uncertainty to estimate the order of dependency (Chatfield, 1973). In general, sequence based analysis seems to suffer from large data set requirements, making it more likely that behavior organization will be obscured. To accurately assess the degree of organization, the assumption of stationarity must not be violated. Only under rare circumstances will this be true for the kind of behaviors presented here. However, the techniques suggested above are useful in locating linked behaviors. The auto- and cross-association technique served best to assess variation among observation periods since data requirements for this technique are small.

We are told by Bartholomew (1982) that a study's results should be viewed from several biological levels, both above and below the level from which the study sprang. It is easy to imagine extending this line of research to brain structures whose interactions control the overt behaviors discussed; many neuroethologists have taken such a route. This is a reductionist approach aimed primarily at proximate factors (Hailman, 1982). It is more difficult to understand why one set of behavior patterns, determined empirically, should be more advantageous to an individual than another set, to us perhaps equally logical. While

this is also couched in proximate terms, its solution is more elusive due largely to difficulties in measuring the effects of a set of behavior patterns (an animal's "character") on lifetime fitness. Several avenues of research are directed at comprehending behavior at this level, e.g., optimal foraging and mate selection. Unfortunately, little is known about the characteristics of one set of non-goal directed behavior patterns that might make them superior to another set.

In the data discussed here, one might ask why the behavior patterns occur with any particular level of predictability. More specifically, one can ask what the advantage is for a turtle to follow the empirically determined "rules" described in this study and not others. Is it a compromise between minimizing energy expenditure and maximizing benefits that might come from social interactions or investigatory behavior? Perhaps increased predictability would make an animal more susceptible to predation or put it at a social disadvantage (Krebs and Dawkins, 1984). More variability might adversely affect performance, putting an individual at a competitive disadvantage with conspecifics. Questions such as these must also be addressed if one is to understand the "rules" governing patterns of behavior.

LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49, 227-267.

Andersson, M. 1974. Temporal graphical analysis of behaviour sequences. Behaviour 51, 38-48.

Bartholomew, G.A. 1982. Scientific innovation and creativity: A zoologist's point of view. Amer. Zool. 22, 227-235.

Bekoff, M. 1977. Quantitative studies of three areas of classical ethology: Social dominance, behavioral taxonomy, and behavioral variability. *In* Hazlett, B.A. (Ed.). Quantitative methods in the study of animal behavior. Academic Press, N.Y. Pp. 1-46.

Biedermann, B.P. 1988. A comparative study of the development of motor patterns associated with prey capture by leopard frogs of the *Rana pipiens* complex (Anura: Ranidae) Master's Thesis. University of Tennessee. 57 pp.

Bishop, Y.M.M., S.E. Fienberg and P.W. Holland. 1975. Discrete multivariate analysis: Theory and practive. 557 pp.

Chatfield, C. 1973. Statistical inference regarding Markov chain models. Appl. Stat. 22, 7-20.

Cooper, W.E. 1977. Information analysis of agonistic behavioral sequences in male iguanid lizards, *Anolis carolinensis*. Copeia 1977, 721-735.

Cooper, W.E. 1979. Variablility and predictability of courtship in *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). J. of Herpetol. 13, 233-243.

Crane, V.R. 1978. On fitting low-order Markov chains to behaviour sequences. Anim. Behav. 26, 332-338.

Dawkins, M. 1983. The organization of motor patterns. *In* Halliday, T.R. and P.J.B. Slater (Eds.). Animal Behaviour, vol. 1: Causes and effects. W.H. Freeman and Co., N.Y. Pp. 75-99.

Dawkins, R. 1976. Hierarchical organization: A candidate principle for ethology. *In* Bateson, P.P.G. and R.A. Hinde (Eds.). Growing points in ethology. Cambridge University Press, Cambridge. Pp. 7-54.

Dawkins, R. and M. Dawkins. 1973. Decisions and the uncertainty of behaviour. Behaviour 45, 83-103.

Dawkins, R. and M. Dawkins. 1976. Hierarchical organization and postural facilitation: rules for grooming in flies. Anim. Behav. 24, 739-755.

Delius, J.D. 1969. A stochastic analysis of the maintenance behaviour of skylarks. Behaviour 33, 137-178.

Douglas, J.M. and A.L. Tweed. 1979. Analyzing the patterning of a sequence of discrete behavioural events. Anim. Behav. 27, 1236-1252.

Fagen, R.M. and D.Y. Young. 1978. Temporal patterns of behavior: Durations, intervals, latencies, and sequences. *In* Colgan, P.W. (Ed.). Quantitative Ethology. John Wiley and Sons, N.Y. Pp. 79-114.

Fentress, J.C. and F.P. Stilwell. 1973. Grammar of a movement sequence in inbred mice. Nature 244, 52-53.

Haccou, P., H. Dienske and E. Meelis. 1983. Analysis of time- inhomogeneity in Markov chains applied to mother-infant interactions of rhesus monkeys. Anim. Behav. 31, 927-945.

Hailman, J.P. 1982. Ontogeny: Toward a general theoretical framework for ethology. *In* Bateson, P.P.G. and P.H. Klopfer (Eds.). Perspectives in ethology, vol. 5. Plenum Press, N.Y. Pp. 133-189.

Heiligenberg, W. 1973. Random processes describing the occurrence of behavioural patterns in a cichlid fish. Anim. Behav. 21, 169-182.

Hinde, R.A. 1973. On the design of check-sheets. Primates 14 (4), 393-406.

Hines, W.W. and D.C. Montgomery. 1980. Probability and statistics in engineering and management science. John Wiley and Sons, N.Y. 634 pp.

Kramer, M. and U. Fritz. 1989. Courtship of the turtle, *Pseudemys nelsoni*. J. Herpetol. 23, 84-86.

Krebs, J.R. and R. Dawkins. 1984. Animal signals: Mind- reading and manipulation. *In* Krebs, J.R. and N.B. Davies (Eds.). Behavioural ecology: An evolutionary approach, 2nd ed. Pp. 380-402.

Lemon, R.E. and C. Chatfield. 1971. Organization of song in cardinals. Anim. Behav. 19, 1-17.

Machlis, L. 1977. An analysis of the temporal patterning of pecking in chicks. Behaviour 73, 1-61.

Machlis, L., P.W.D. Dodd and J.C. Fentress. (1985) The pooling fallacy: Problems arising when individuals contribute more than one observation to the data set. Z. Tierpsychol. 68, 201-214.

Metz, H. 1974. Stochastic models for the temporal fine structure of behaviour sequences. *In* McFarland, D.J. (Ed.). Motivational control systems analysis. Academic Press, N.Y. Pp. 5-86.

Oden, N. 1977. Partitioning dependence in nonstationary behavioral sequences. *In* Hazlett, B.A. (Ed.). Quantitative methods in the study of animal behavior. Academic Press, N.Y. Pp. 203-220.

Slater, P.J.B. 1973. Describing sequences of behavior. *In* Bateson, P.P.G. and P.H. Klopfer (Eds.). Perspectives in Ethology, Vol. I., Plenum Press, N.Y. Pp. 131-153.

Slater, P.J.B. and J.C. Ollason. 1972. The temporal pattern of behaviour in isolated male zebra finches. Transition analysis. Behaviour 42, 248-269.

Steinberg, J.B. 1977. Information theory as an ethological tool. *In* Hazlett, B.A. (Ed.). Quantitative methods in the study of animal behavior. Academic Press, N.Y. Pp. 47-74.

van der Kloot, W. and M.J. Morse. 1975. A stochastic analysis of the display behavior of the red-breasted merganser (*Mergus serrator*). Behaviour 54, 181-216.

van Rhijn, J.G. 1977. The patterning of preening and other comfort behaviour in a herring gull. Behaviour 73, 71-108.

APPENDIX

TABLES AND FIGURES

Table 1. Summaries of observation periods and sums for each turtle.

Observation ID	Duration (min)	Number of behaviors
T1-11/12	30	99
T1-11/14	60	177
T1-12/27	60	154
	150	430
T2-11/13	30	100
T2-12/29	20	61
T2-4/6	40	155
T2-4/7	60	175
	150	491
T3-11/16	60	188
T3-11/20	30	63
	90	251
T4-11/17	60	288
T4A-11/22	30	154
T4B-11/22	30	98
T4-12/5	60	223
T4-12/28	20	58
	200	821

Note: Observation ID consists of turtle ID and date of observations.

Table 2. Some common sequences of behaviors by each turtle (*Pseudemys nelsoni*).

Turtle ID	Sequence	Frequency
1	212	75
	2124	11
	717	8
	271727	3
2	212	40
	21212	11
	2124	19
	246	12
	246246	3
	242424	7
	383	17
	3838383	3
3	212	27
	21212	7
	2124	13
	1212124	3
	27272	4
	86868686	6
4	212	71
	21212	14
	124	48
	2124	33
	1246	18
	21246	14
	6868	10

Note: Behaviors are: 1 = **surface**, 2 = **swim**, 3 = **crawl**, 4 = **to bottom**, 5 = **still**, 6 = **eat**, 7 = **interact (init)**, 8 = **interact (recip)**.

Table 3. Comparison of proportion of each behavior frequency of *Pseudemys nelsoni* with that predicted by projecting the first order transition matrix.

Turtle	Behavior	Frequency	Proportion	Stationary Distribution
1	1	125	0.29070	0.29429
	2	134	0.31163	0.31098
	3	27	0.06279	0.06322
	4	45	0.10465	0.10430
	5	12	0.02791	0.02594
	6	38	0.08837	0.08878
	7	29	0.06744	0.06590
	8	20	0.04651	0.04659
2	1	72	0.14664	0.14591
	2	141	0.28717	0.28734
	3	72	0.14664	0.14492
	4	81	0.16497	0.16795
	5	25	0.05092	0.05110
	6	26	0.05295	0.05309
	7	36	0.07332	0.07384
	8	38	0.07739	0.07584
3	1	36	0.14343	0.14429
	2	74	0.29482	0.29493
	3	26	0.10359	0.10371
	4	27	0.10757	0.10889
	5	12	0.04781	0.04800
	6	24	0.09562	0.09551
	7	17	0.06773	0.06897
	8	35	0.13944	0.13571
4	1	148	0.18408	0.18496
	2	217	0.26990	0.26991
	3	67	0.08333	0.08340
	4	119	0.14801	0.14871
	5	35	0.04353	0.04148
	6	109	0.13557	0.13544
	7	27	0.03358	0.03379
	8	82	0.10199	0.10231

Table 4. Results of G-tests for models of independence of individual matrices of lags 0-10 and for the model of no difference among turtles (*Pseudemys nelsoni*).

	Individual Turtles								Differences among Turtles	
	1		2		3		4			
Lag	G	df	G	df	G	df	G	df	G	df
0	85.5**	13	280.1**	27	51.9**	8	507.9**	30	180.4**	10
1	189.3**	18	184.9**	33	130.7**	16	325.5**	32	143.5**	44
2	138.2**	15	87.4**	30	77.2**	14	111.2**	35	168.2**	50
3	122.8**	15	67.1**	29	30.4**	13	63.8**	33	161.7**	54
4	76.0**	13	69.6**	24	32.9**	16	47.2*	32	174.7**	56
5	65.6**	14	36.9*	22	26.3*	13	46.0	32	195.2**	72
6	45.7**	12	50.5**	22	8.8	11	49.5*	31	176.8**	69
7	37.2**	11	37.3*	20	5.0	3	42.5	31	151.7**	58
8	42.4**	11	52.5**	21	2.9	4	44.8	31	170.4**	57
9	48.0**	12	26.8	22	10.3	8	56.8*	35	not tested	
10	43.8**	12	75.7**	34	10.5	8	60.5**	34	not tested	

* $p < .05$
** $p < .01$

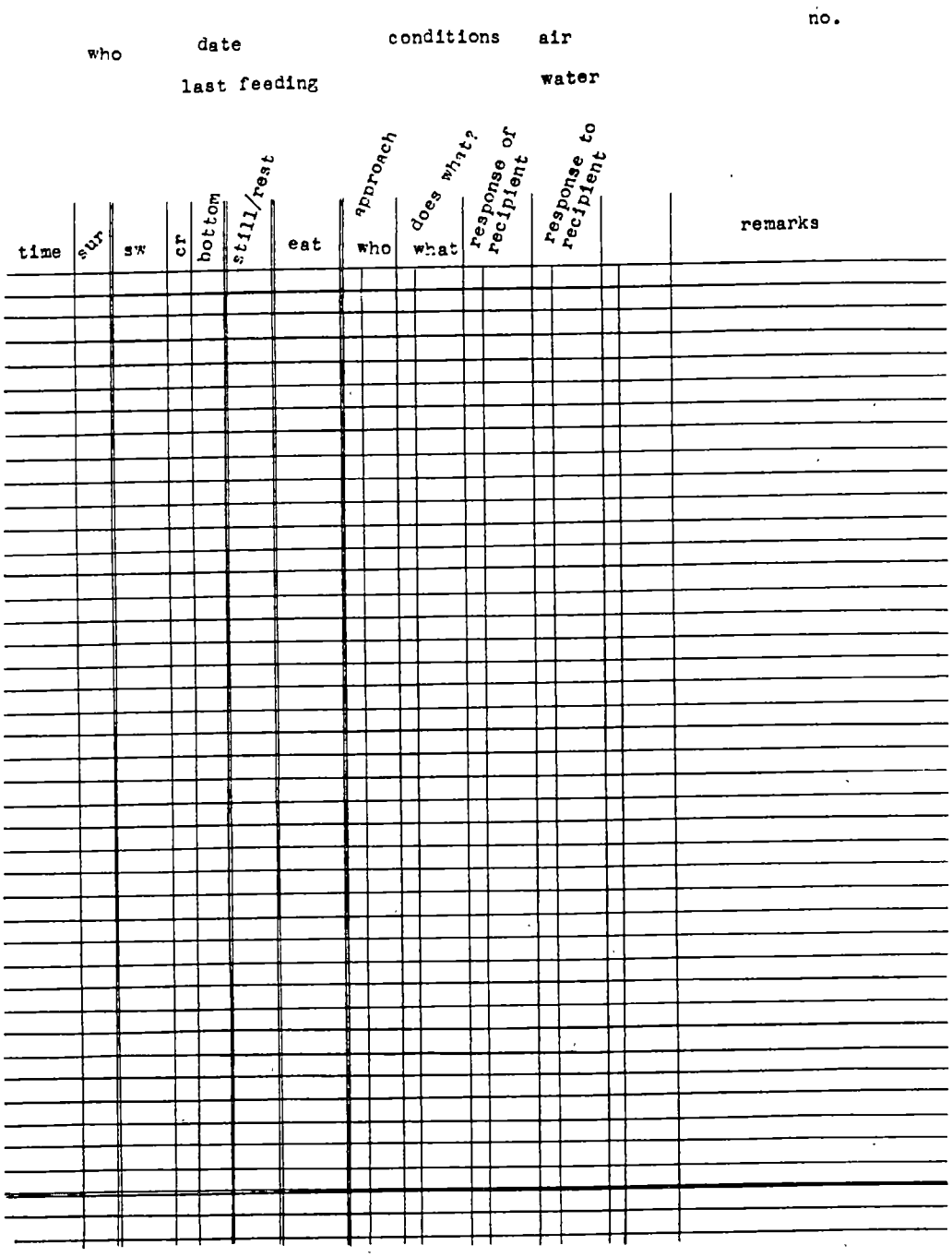

Figure 1. Check-sheet used to record sequences of behavior of *Pseudemys nelsoni*. A new line was started every 30 s. Behaviors were numbered within the 30 s interval so that the order of behaviors could be extracted. If a line became too crowded before the end of the 30 s interval, a new line was started with an X entered under time.

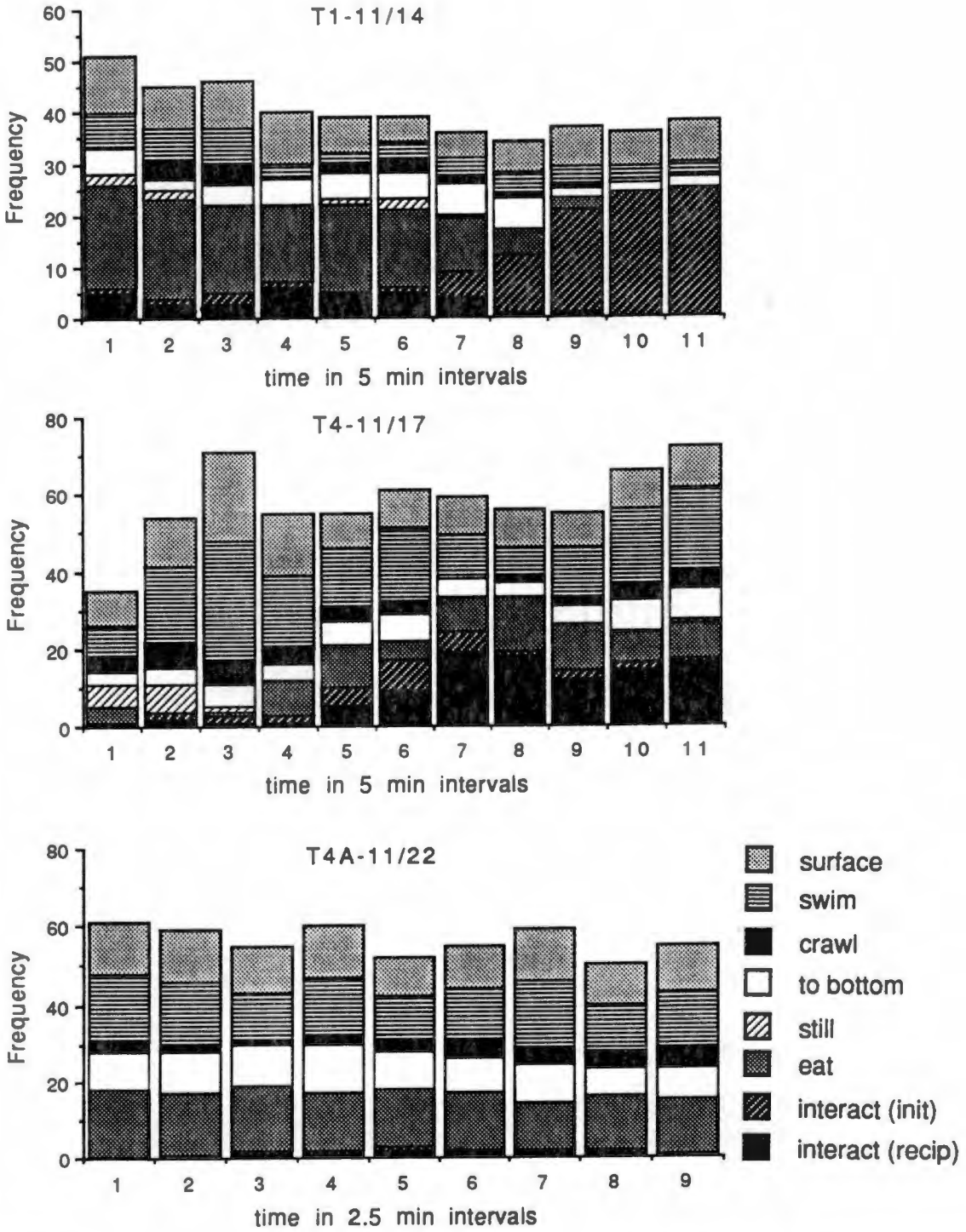

Figure 2. Three examples of sliding sums. Ten min sums are depicted in 5 min intervals for longer observation periods and every 2.5 min for shorter ones. The observation period identification above each histogram gives turtle ID and date of observations.

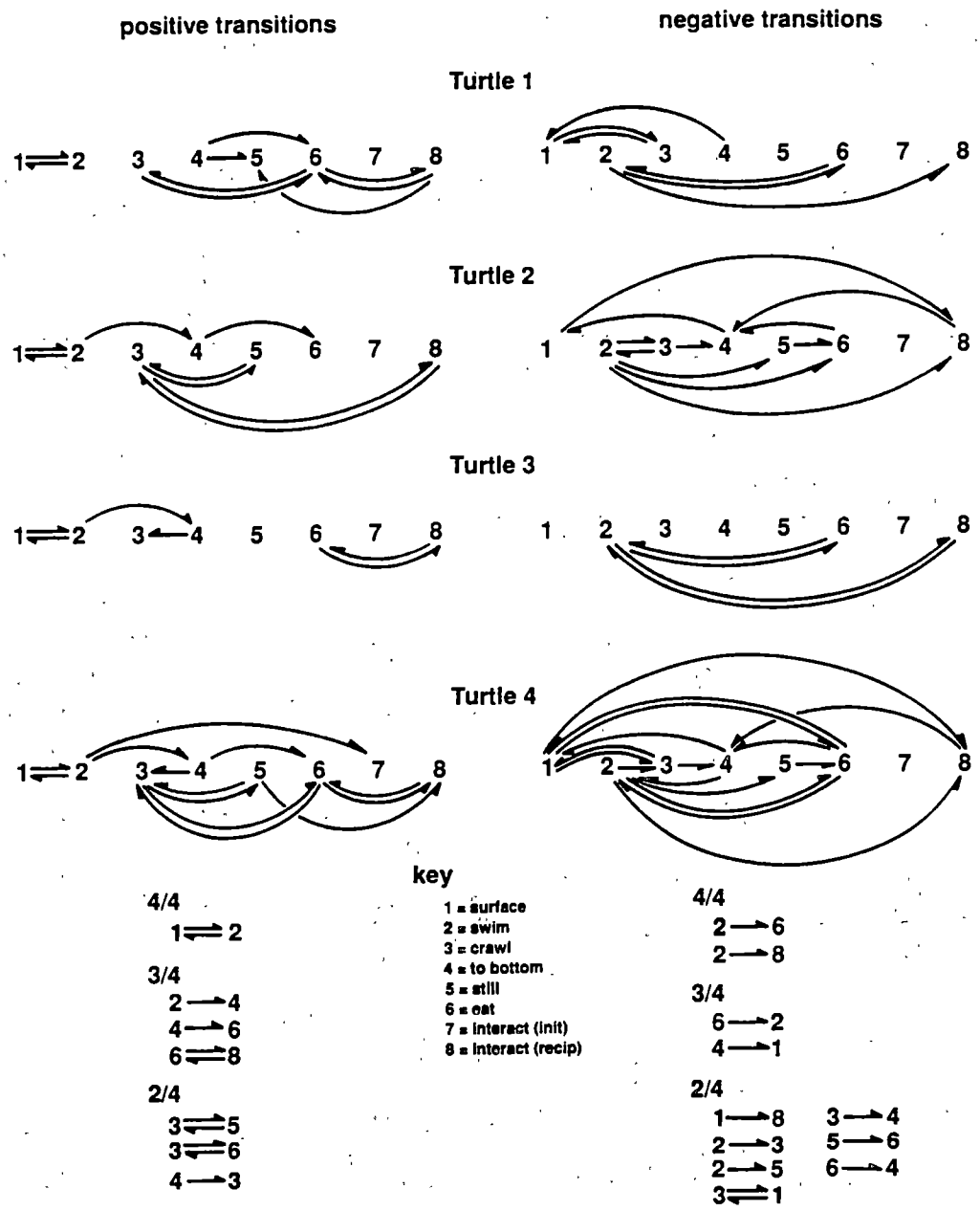

Figure 3. Significant first order transitions for each of the turtles (*Pseudemys nelsoni*). Transitions that occurred more frequently than expected (positive transitions) are diagrammed on the left, less frequently (negative transitions) on the right. Summaries of significant transitions common to all turtles, three of four, and two of four are given beneath the diagrams.

Figure 4. Lagged frequencies of **surface** following each of the eight behaviors for each of the four turtles (*Pseudemys nelsoni*). In lag 0 histogram bars, there are no intervening behaviors, in lag 1 there is one, etc. Since repeated behaviors were eliminated, the lag 0 **surface-surface** transition is a structural zero. Filled bars and arrows beneath a bar or zero indicate chi-square deviates less than -1.96 or greater than 1.96 in the individual turtle transition matrices. A plus or minus above a bar indicates a χ^2 deviate of less than - 1.96 or greater than 1.96 when comparing turtles. For example, Turtle 1 was more likely to follow **swim** with **surface** than other turtles at lag 0.

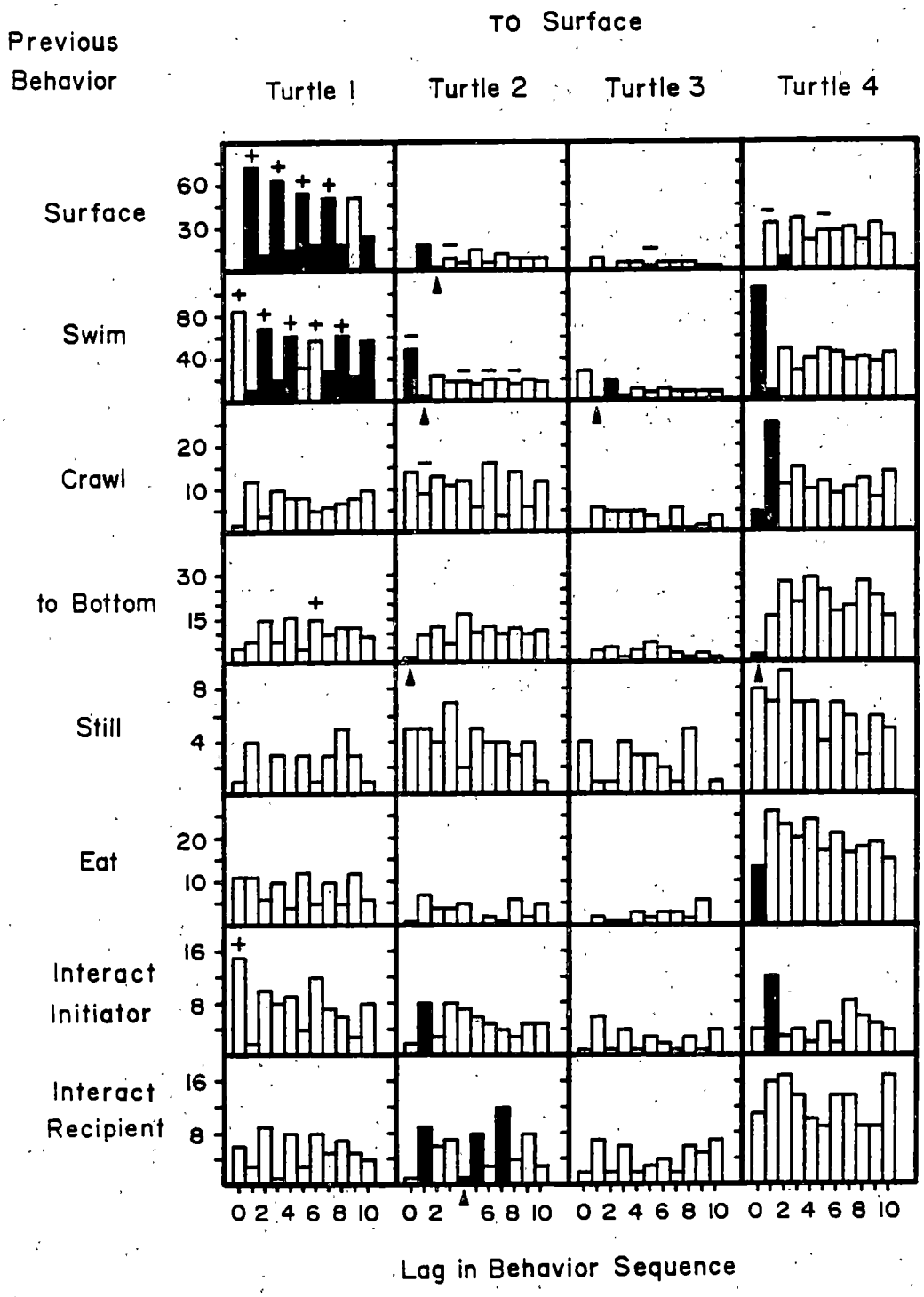
TO Surface
Previous Behavior
Turtle 1
Turtle 2
Turtle 3
Turtle 4
Surface
Swim
Crawl
to Bottom
Still
Eat
Interact Initiator
Interact Recipient
60
30
80
40
20
10
30
15
8
4
20
10
16
8
16
8
0 2 4 6 8 10
Lag in Behavior Sequence

Figure 4

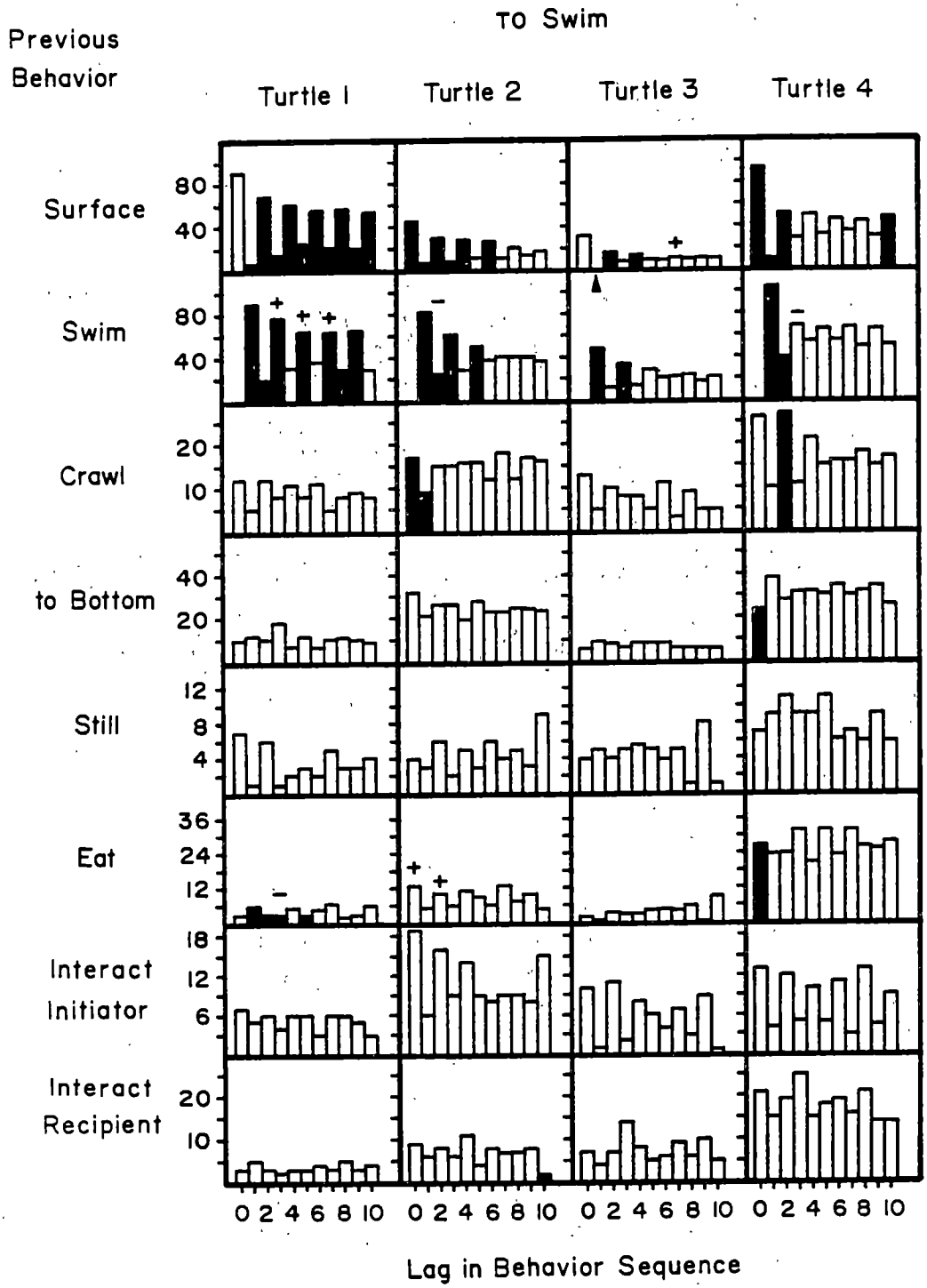

Figure 5. Lagged frequencies of **swim** following each of the eight behaviors for each of the four turtles, *Pseudemys nelsoni*. See the legend of Fig. 4 for details.

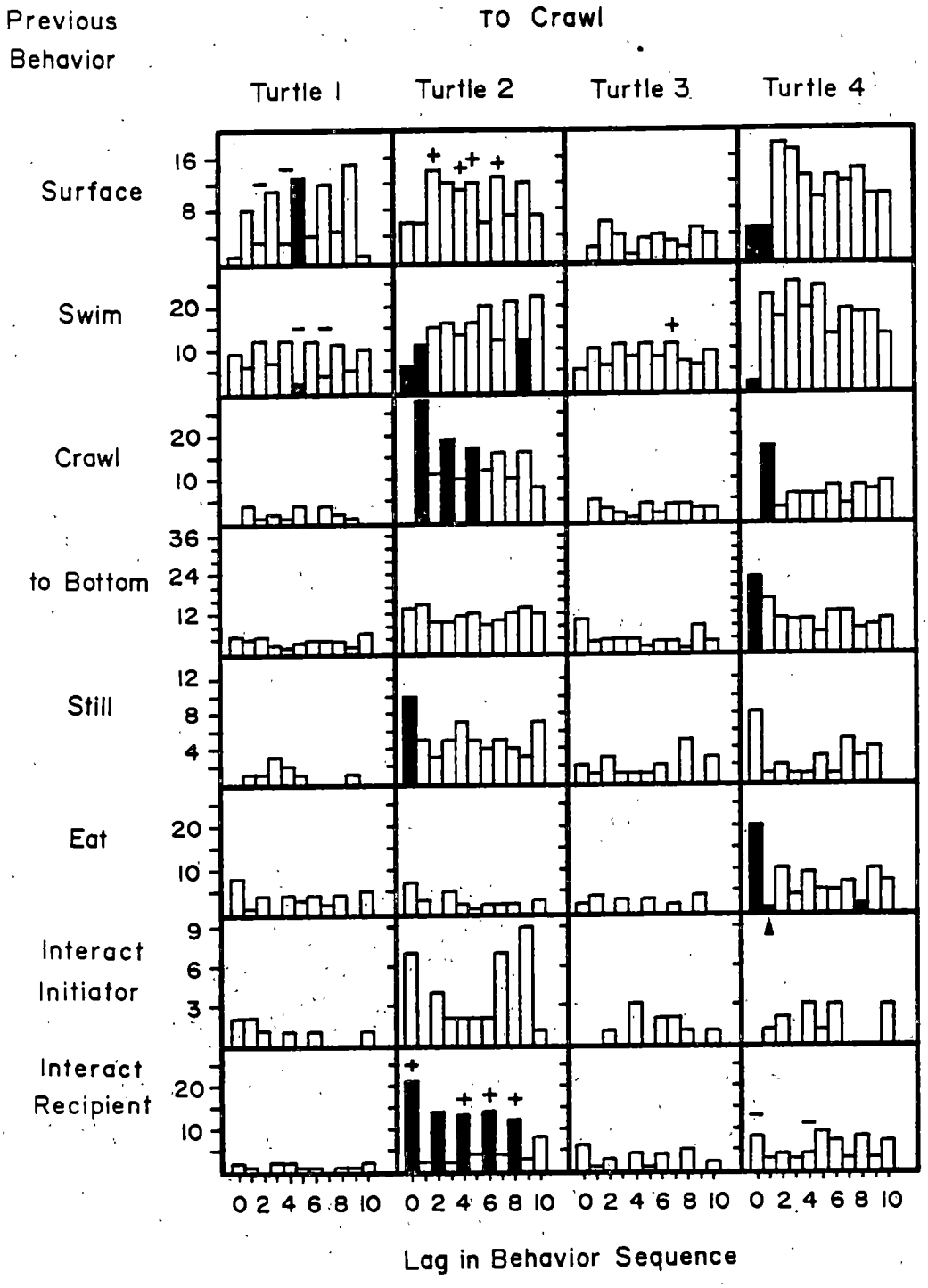

Figure 6. Lagged frequencies of **crawl** following each of the eight behaviors for each of the four turtles, *Pseudemys nelsoni*. See the legend of Fig. 4 for details.

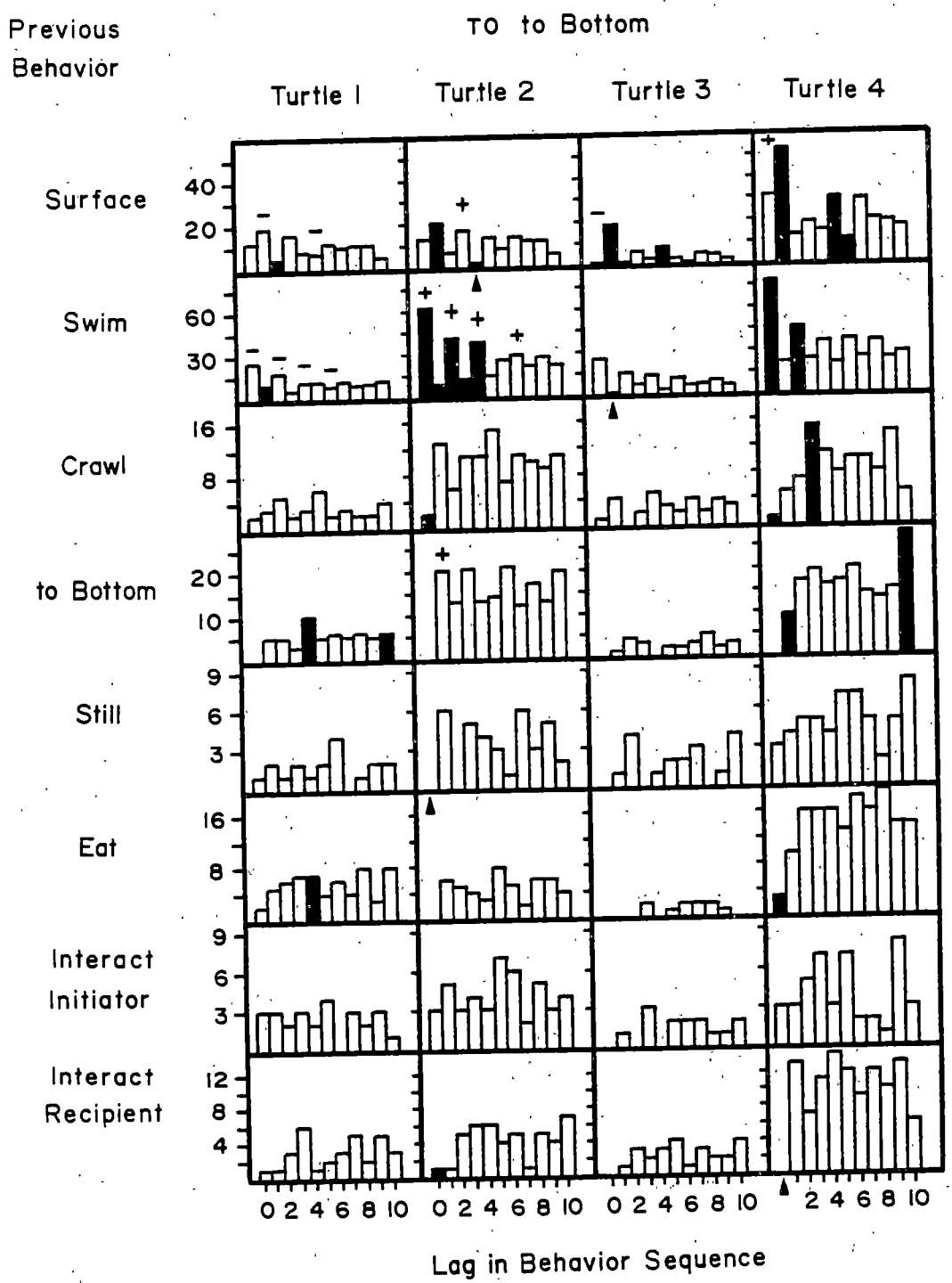

Figure 7. Lagged frequencies of **to bottom** following each of the eight behaviors for each of the four turtles, *Pseudemys nelsoni*. See the legend of Fig. 4 for details.

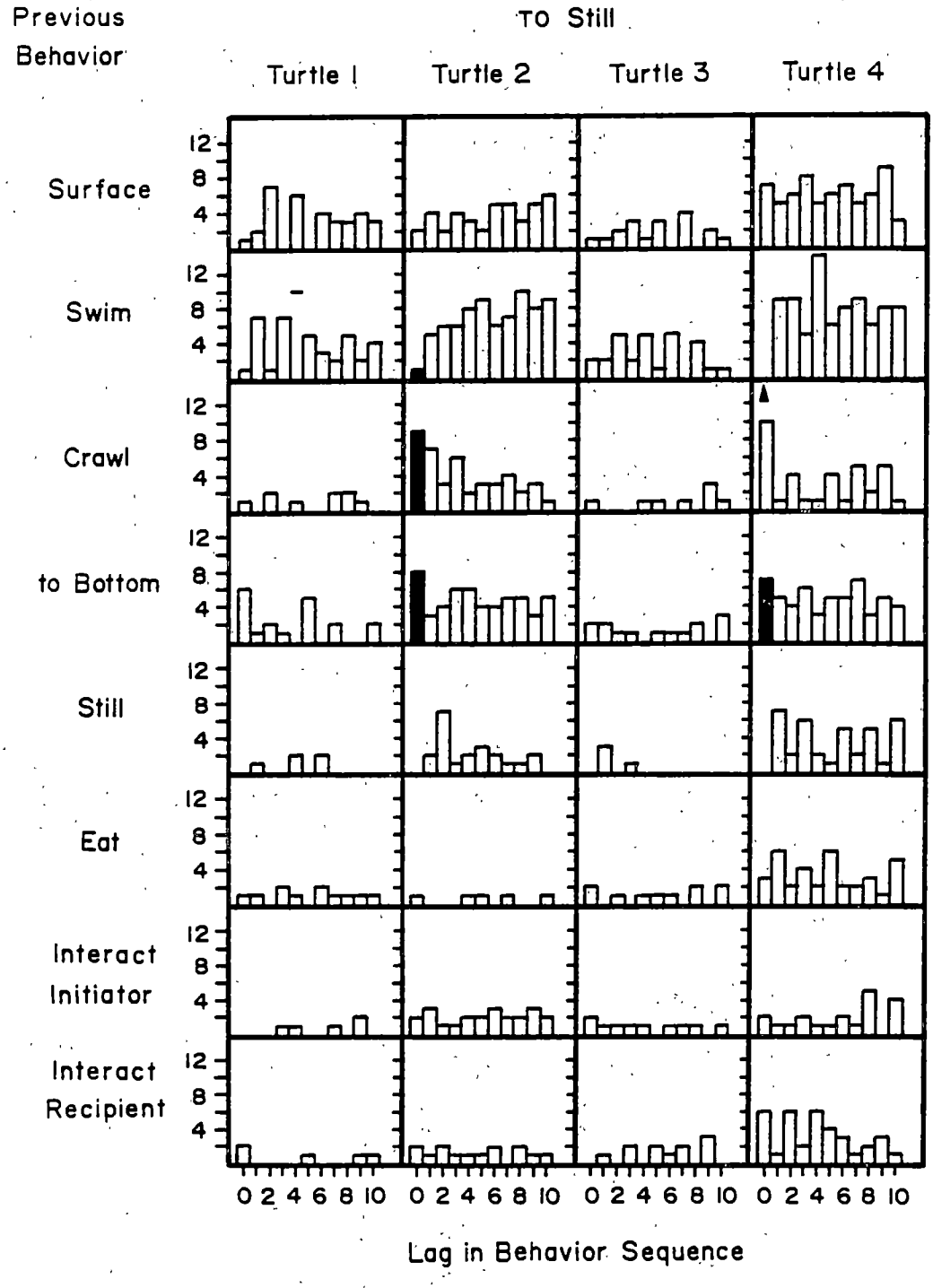

Figure 8. Lagged frequencies of **still** following each of the eight behaviors for each of the four turtles, *Pseudemys nelsoni*. See the legend of Fig. 4 for details.

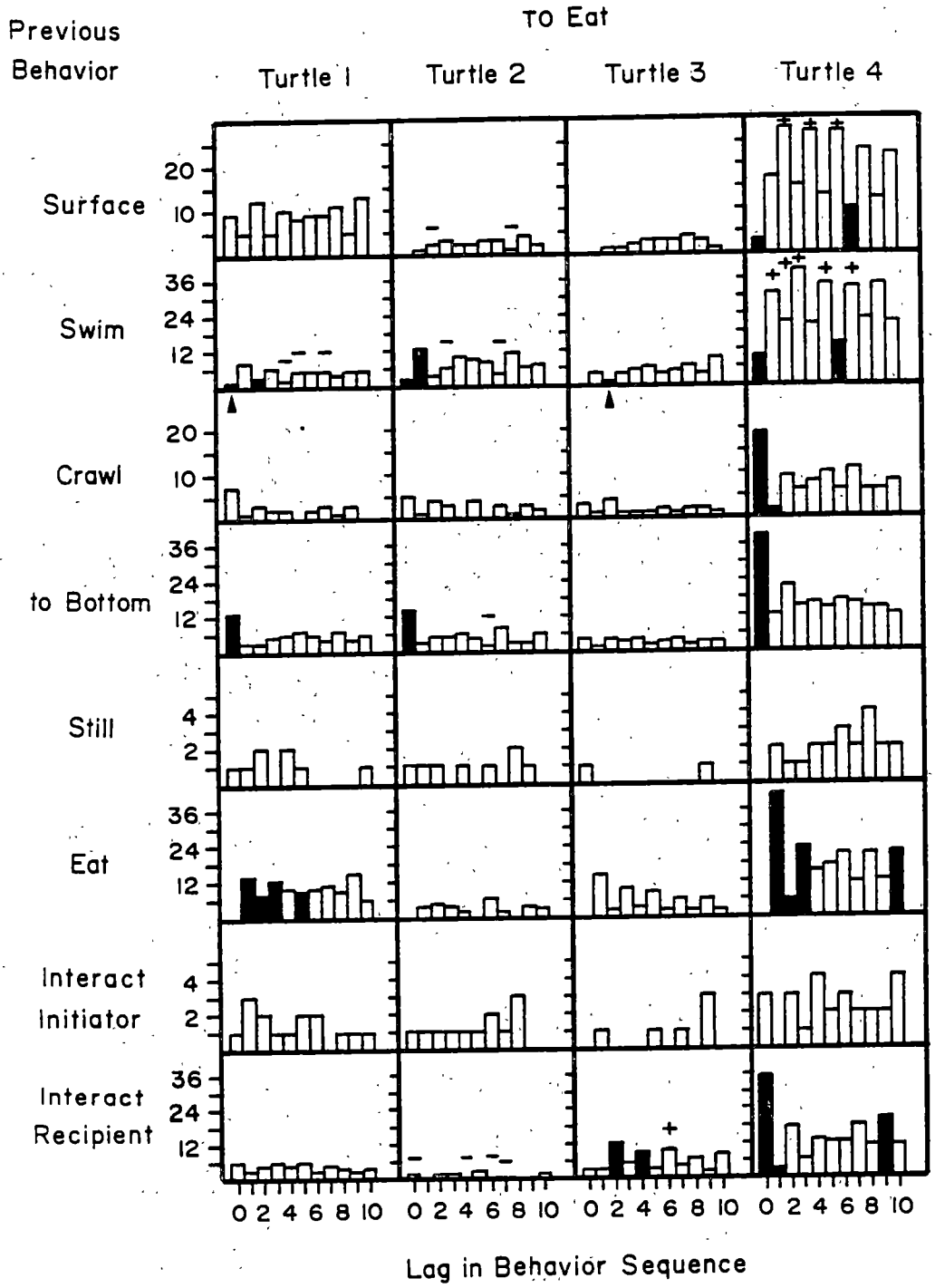

Figure 9. Lagged frequencies of **eat** following each of the eight behaviors for each of the four turtles, *Pseudemys nelsoni*. See the legend of Fig. 4 for details.

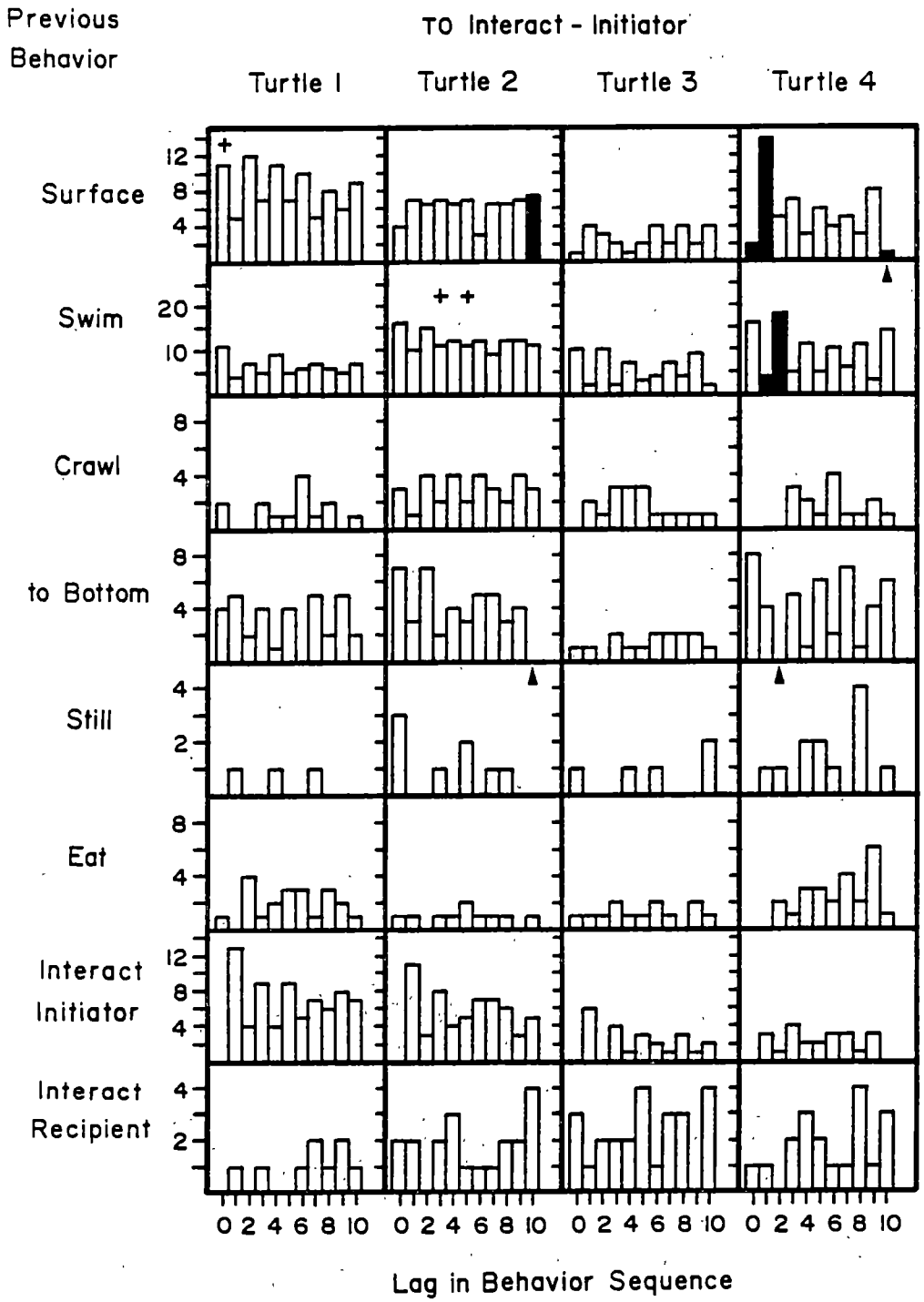

Figure 10. Lagged frequencies of **interact** (**init**) following each of the eight behaviors for each of the four turtles, *Pseudemys nelsoni*. See the legend of Fig. 4 for details.

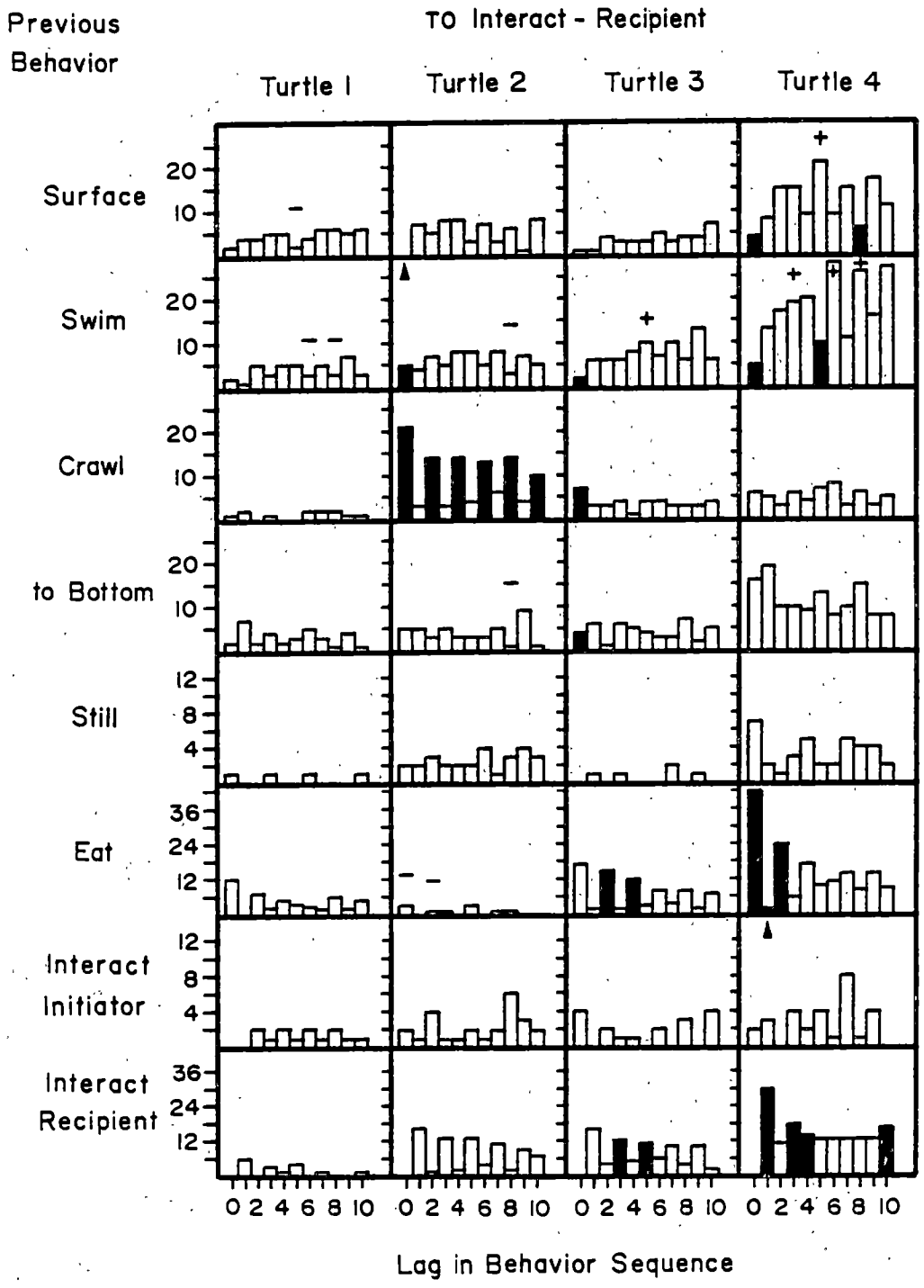

Figure 11. Lagged frequencies of **interact (recip)** following each of the eight behaviors for each of the four turtles, *Pseudemys nelsoni*. See the legend of Fig. 4 for details.

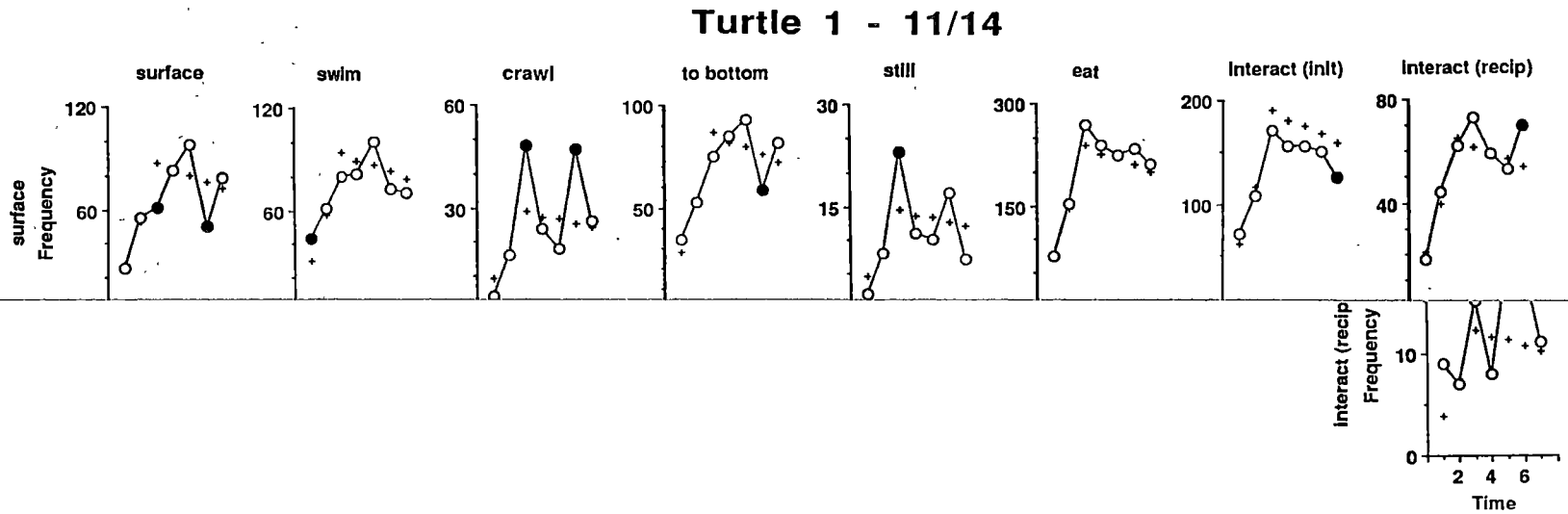

Figure 12. Auto- and cross-associations among all behavior pairs. These are given for one observation period, T1-11/14, of one juvenile *Pseudemys nelsoni* turtle with within 60 s, 60-150 s, 150-300 s, 300-450 s, 450-600 s, 600-750 s, and 750-900 s separating the behaviors. Filled circles are association frequencies that differ significantly from expected (small crosses).

Figure 13. Auto- and cross-associations of behavior pairs 1 - 18. The time period (X-axis), observation session (top row), and the direction and magnitude of the deviations (black bars) are given. Time periods correspond to within 60 s, 60-150 s, 150-300 s, 300-450 s, 450-600 s, 600-750 s, and 750-900 s separating the behaviors. Deviations illustrated are Freeman-Tukey deviates, the magnitudes correspond to $p = 0.05$, 0.01, and 0.001. Dotted lines indicate expected cell frequencies removed from the analysis due to low frequencies.

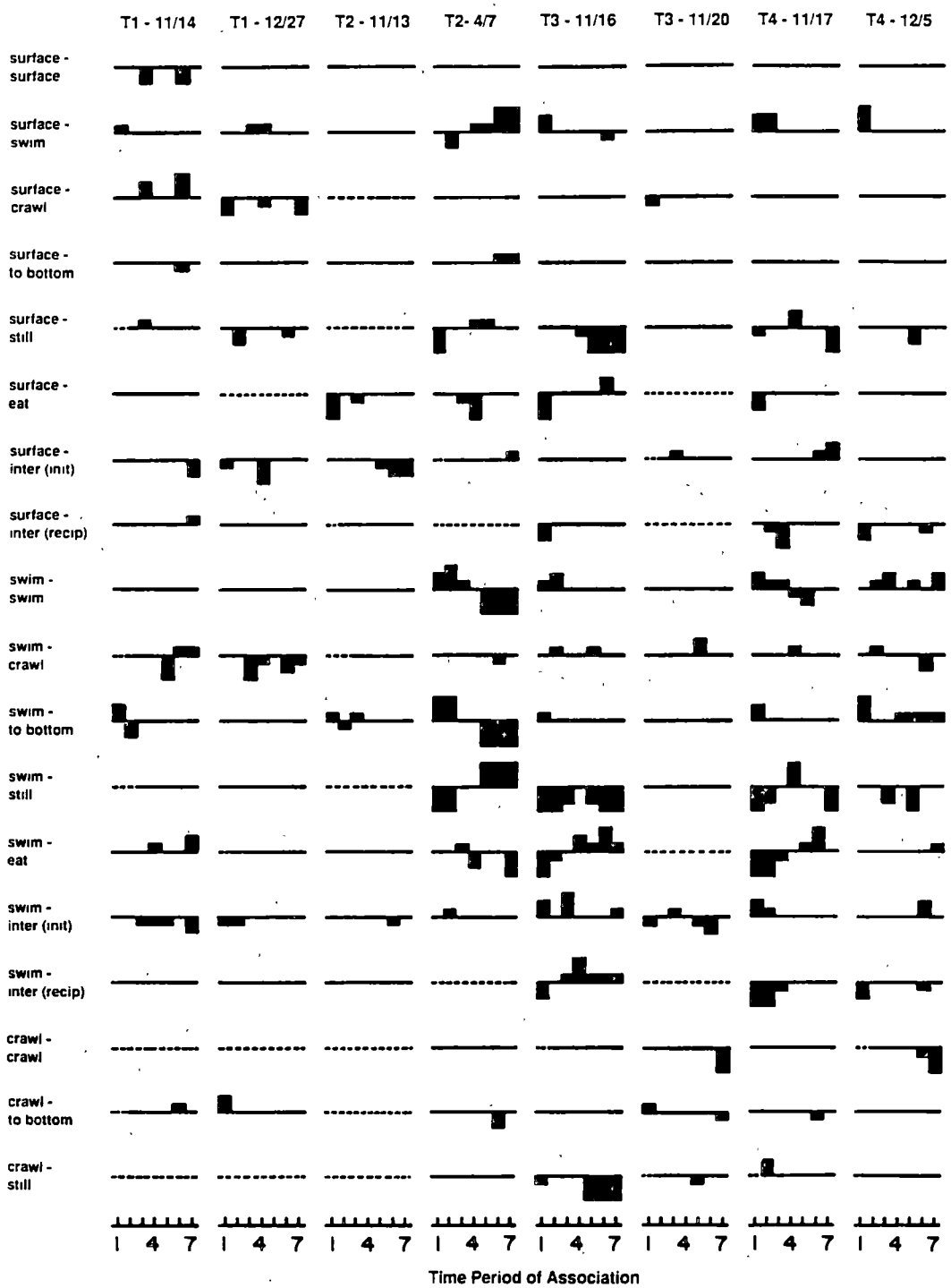
T1 - 11/14
T1 - 12/27
T2 - 11/13
T2- 4/7
T3 - 11/16
T3 - 11/20
T4 - 11/17
T4 - 12/5
surface - surface
surface - swim
surface - crawl
surface - to bottom
surface - still
surface - eat
surface - inter (init)
surface - inter (recip)
swim - swim
swim - crawl
swim - to bottom
swim - still
swim - eat
swim - inter (init)
swim - inter (recip)
crawl - crawl
crawl - to bottom
crawl - still
1 4 7
Time Period of Association

Figure 13

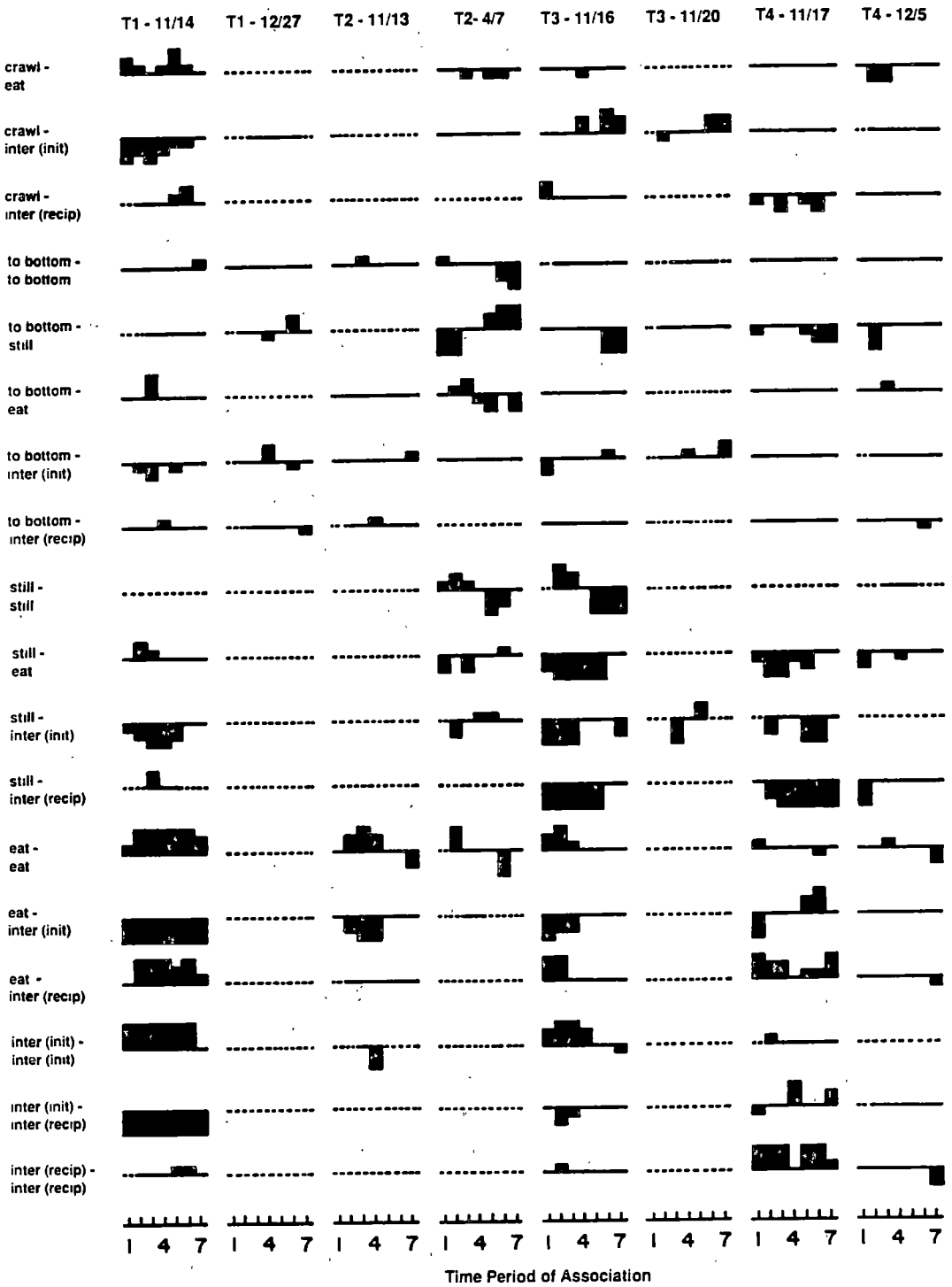

Figure 14. Auto- and cross-associations behavior pairs 19 - 36. See Fig. 13 for details.

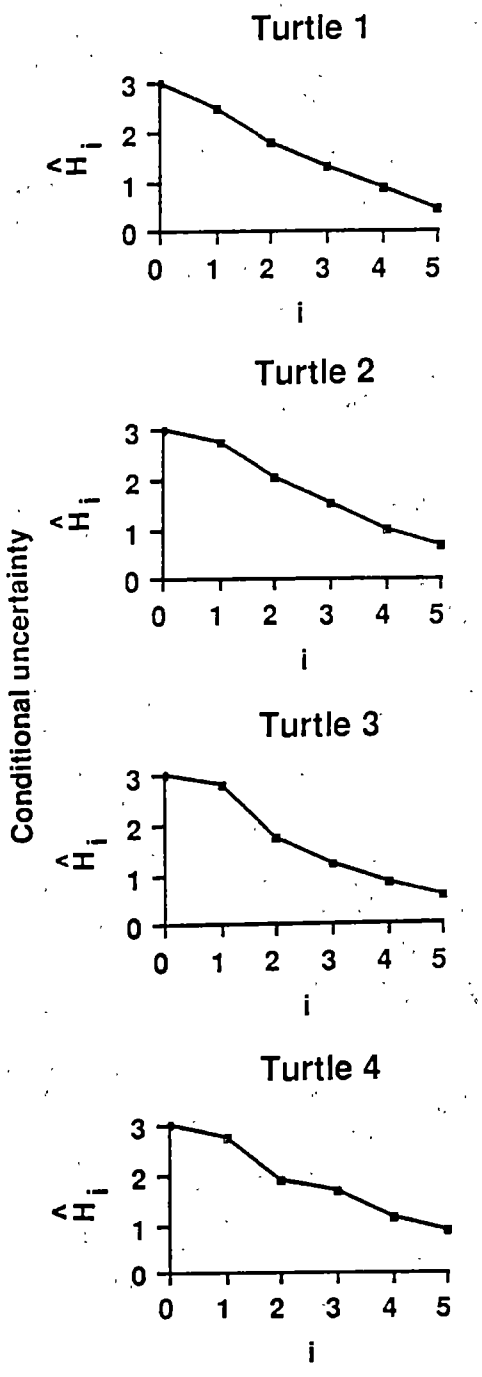

Figure 15. Graphs of conditional uncertainty (H_i) vs. i for each turtle (*Pseudemys nelsoni*). An i of zero corresponds to the model that behaviors are equiprobable. An i of one corresponds to the model that behaviors occur at random but with different frequencies. An i of two corresponds to a first order Markov chain, etc. The differences in conditional uncertainty between models reflect the reduction in uncertainty by using the higher order model.

PART 4

THE BASKING PATTERN OF *PSEUDEMYS NELSONI*

CHAPTER 1

INTRODUCTION

Elevation of body temperature generally is believed to be the primary function of basking in semi-aquatic turtles (Sturbaum, 1982). In addition, basking may assist digestion, skin maintenance, and vitamin synthesis (Lovich, 1984; Chessman, 1987). Behavioral studies of basking have addressed social interactions (Bury and Wolfheim, 1973; Bury et al., 1979; Lovich, 1984), maintenance behaviors (Auth, 1975; Litwin, 1975; Vogt, 1978), and the relationship between basking frequency and environmental variables (e.g., Auth, 1975).

Atmospheric basking (Moll and Legler, 1971) in semi-aquatic turtles is amenable for ethological field research because animals are easy to observe and movements occur intermittently. For these reasons basking animals are also good subjects for ecologically oriented studies (e.g., Boyer, 1965; Auth, 1975; Chessman, 1987; Crawford et al., 1983; Lovich, 1984; Spotila et al., 1984).

The intent of this study was to quantify the behaviors of atmospheric basking *Pseudemys nelsoni* (Emydidae) and compare them with those of other turtles, in particular, *Trachemys scripta* (Auth, 1975) and *Chrysemys picta* (Litwin, 1975).

CHAPTER 2

MATERIALS AND METHODS

Study Site and Subjects

All basking observations were made at Rock Springs run, described in Part 2. Data were collected on the behavior of turtles basking on three logs in the study site. One log was used primarily by adult male and juvenile *Pseudemys nelsoni*. The others were used by all age and sex classes other than small juveniles and by both *P. nelsoni* and *P. floridana*. One of the larger logs remained shaded until midmorning, the other two were directly exposed for most of the day. On weekend mornings, when canoe traffic was heaviest, basking animals were disturbed as often as every ten min. In contrast, canoe traffic on weekday afternoons was light or nonexistent.

Many individuals in the study site were marked permanently with holes drilled through the marginals. They were also given temporary paint marks, readable through binoculars, but these only lasted a few months (Kramer, 1986). Thus, identification from one observation period to another was not possible for many turtles. Some unmarked individuals that left and returned later to continue basking could be reliably identified within the observation period due to a combination of characters. The most useful were dark markings on the ventral surfaces of marginals 4 - 7 and the bridge; also size, shape, sex, species, general coloration, and mutilations, such as missing part of the tail, foot or edge of carapace. There were no obvious differences between the behavioral basking patterns of *P. nelsoni* and *P. floridana* and, since few observations were made on *P. floridana*, data taken on adults of both species were combined. Analyses were performed with and without the

additional *P. floridana* data with identical results. The data discussed below include observations of *P. floridana.*

Observation Procedures

Observations were made only on during favorable conditions (i.e., sunny days) through 7 x 35 binoculars. The distributions of daily and yearly observation periods are given in Part 2. Movements and posture changes of one or two focal animals were continuously recorded during the observation period with the behaviors of additional animals recorded if this did not interfere with recording the behavior of the focal animal(s). Behaviors used in this analysis (Table 1) are a subset of the behaviors described for basking *P. nelsoni* in Part 2. The focal animal was the first adult to emerge onto the log in a position that permitted unobstructed viewing after I had settled into an observation position. Observations were made either from a canoe anchored near the opposite bank, about 25 m away, or from the densely shaded woods, about 17 m away, which served as a natural blind. The behaviors of the focal animal were recorded by hand until it went into the water. A later emerging individual whose behaviors had been fairly well monitored was then followed.

Data Analysis

An animal's recent basking history could influence subsequent basking behavior. However, lumping data of animals with differing recent basking histories was unavoidable since most individuals' basking history was unknown. A basking session began when an individual emerged onto the basking site, whether or not it had previously basked during

the observation period. All focal animals were *Pseudemys nelsoni*. Emergence time was standardized to zero and the occurrence of all subsequent posture changes reckoned as the time elapsed since the turtle emerged. Behaviors resulting from obvious human disturbance were not used in the analysis. At this study site the majority of basking sessions were ended by human disturbance.

These data were used to examine the relationship between certain postures and time spent basking (initial n = 24). The frequency distributions were converted to percentages and two-sided 95% confidence intervals calculated (Rohlf and Sokal, 1981). I considered the head and four limb postures of each turtle (if visible) as independent data (initial front leg n = 46, initial rear leg n = 47). Data limitations precluded useful statistics much past the first 60 min.

The focal animal data were then combined with all additional data taken on animals other than the focal individual for which emergence times were known (initial n = 42). This larger data set was used to determine if the distribution of acts in time were independent of the distribution of the duration of basking sessions. The latter distribution was calculated as the average number of turtles observed basking for 0-15 min, 15-30 min, etc. (Fig. 1b) and adjusted using the total of each of the acts to obtain the expected frequencies. Since many basking sessions were interrupted by human disturbance, the distribution of basking durations (Fig. 1b) does not represent the distribution of voluntary or natural basking durations.

The observed frequencies of each act were tested against the expected using the G-test for goodness-of-fit (Sokal and Rohlf, 1981). Cell deviates were examined using the chi-square approximation (Bishop et al., 1975). If the distribution of the act closely followed the expected distribution, the act occurs independently of time, that is, the length of time an animal basked would not be a good predictor of how likely it is to perform the act.

Statistical Validity and Power

An assumption of the null hypotheses for testing the independence of each act in time is that the observed frequencies of the act occur with a characteristic probability (e.g., walking once is more likely than walking five times) but the probability distribution of frequencies for the act is the same throughout the basking session, i.e., the same in all 15 min intervals.

To determine if a G-test could appropriately test these hypotheses, a computer simulation was performed for each of the five acts using Proc IML in SAS (1983). The routine assigned numbers generated randomly from a uniform distribution (from zero to one) to one of several of categories, the categories representing the possible frequencies of the act. For example, there were eight categories of walks since an animal might walk from zero to seven times during a 15 min interval. The probability of a random number falling into each category was determined empirically from the data, thus do not follow any particular mathematical function. For example, the probability of a turtle walking zero times was 0.8095, walking once 0.1201, etc. (Table 2). If the random number generated was 0.5, the number of walks assigned to that turtle for that 15 min interval was zero. If the random number generated was 0.99, three walks were assigned. Under the null hypothesis, the probability of walking zero times is the same for all 15 min intervals, likewise for walking once, twice, etc. However, since the frequencies were produced using a random number generator, the total frequencies of the 15 min intervals could differ greatly, even though the data were generated under the null hypothesis. For this reason, the methodology outlined above can be used to determine if a G-test is appropriate. If the simulated total frequencies among the 15 min intervals do not differ greatly, then the G-test is valid. If they do differ greatly, then a G-test will not be able to discriminate between data

distributed as hypothesized under the null hypothesis or distributed under an alternate hypothesis.

Data were generated representing sample sizes of 4, 8, 16, 32, and 64 turtles for each of the five acts in basking sessions of 10 15-min intervals. The resulting frequencies, summed over turtles for each 15 min interval, were tested for goodness-of-fit against a discrete uniform distribution, created by summing all frequencies for that simulation and dividing by 10, the number of 15 min intervals. One thousand simulated experiments of each sample size were used to assess the validity of the G-test, with William's correction (Sokal and Rohlf, 1981).

To assess the power of the test, a number of distributions under alternative hypotheses were constructed in the manner described above except that the probabilities of performing the act differed among the 15 min intervals. I used exponential functions to differentially change the probabilities of each act in the 10 15-min intervals and simulated seven alternative hypotheses. These ranged from the act being performed at slightly higher frequencies at the beginning of the basking session and negative exponentially decaying to the values drawn from the data to the act being perfomed at moderately higher frequencies at the beginning of the basking session (Fig. 2). These were tested against null hypotheses of equal frequencies among 15 min intervals, as described above. One thousand simulated experiments were used at each sample size to assess power.

CHAPTER 3

RESULTS

Basking Behavior in *Pseudemys nelsoni*

Animals typically emerged on basking sites in full sunlight although they occasionally emerged on shaded logs, especially in the morning. Turtles often remained basking after logs were shaded, the sky became overcast, or during light rain. After arriving to bask, turtles immediately climbed to the upper surface of the log. Most turtles were oriented in the same direction on the basking site and not for maximum sun exposure, probably due to both the physical constraints of basking on logs (Lovich, 1984) and reluctance to face others directly (Lovich, 1984; Vogt, 1978; see Part 2). Piling, when one turtle climbs on top of another, and aggressive behavior were never seen, probably due to relatively uncrowded basking sites.

Marked or recognizable basking individuals were rarely seen to enter the water voluntarily and reappear a few minutes later, described by Lovich (1984) for *Chrysemys picta*. However, reemergence within 30 min or less after a human disturbance was common. Animals that entered the water voluntarily did not exhibit hyperactivity or move about the basking site before entering the water (Auth, 1975, Litwin, 1975); rather, they turned, paused, and walked off the log.

Posture Changes during Basking

The likelihood of a turtle assuming a certain posture was related to the length of time the animal had been basking. Throughout the basking session animals tended to maintain their heads in an elevated position (Fig. 1a) although the percentages of the other two head postures increased with time. The front legs were usually planted on the substrate (Fig. 1a). Retraction of the front legs became more frequent with increased basking time and plateaued at 30 - 40% after about 60 min. The hind legs showed a similar pattern (Fig. 1a) although they were held extended more often than the front legs, 10 - 20% of the time after the first 10 min with a maximum of 30% at 50 min. They were retracted slightly less often than the front legs.

Distribution of Acts in Basking Sessions

Results of simulations

The results of the computer simulations demonstrated that the G statistic for testing goodness-of-fit was appropriate for walks, turns, and extend legs since the null hypotheses were rejected less than 5% of the time, but inappropriate for head rubs and kicks, etc. (Table 3). In the latter two cases, the null hypotheses were rejected far too frequently for the test to have merit. The goodness-of-fit tests for kicks, etc. yielded particularly high rates of rejection, for a sample size of 32, the null hypothesis was rejected for 96.4% of simulated experiments at an $\alpha = 0.05$. The reason that a G-test was valid to test some of the behavior distributions against the null hypothesis but not others is evidently due to the

empirical probability distributions of the behaviors. Unfortunately, it is not known what feature or combination of features of these distributions is responsible.

The power analyses on walks, turns, and extend legs revealed how different the distributions under the alternative and null hypotheses must be for the G-test to reliably differentiate between them (Table 3). The ability to discriminate between a true alternative hypothesis and the null hypothesis depends greatly on sample size but even moderate differences were detectable with a sample size of 32. The results from the computer simulations indicate that the G-test is appropriate to test the null hypotheses that the frequencies of walks, turns, and extend legs are uniformly distributed over the observation period. Additionally, there is good power to detect moderate to large differences in frequencies of these acts among the 15 min intervals for the data collected.

Results of testing for differences among 15 min intervals

The distributions of walks, turns, and extend legs differed significantly ($p < 0.01$) from the expected distributions, suggesting that they are more likely to occur at certain times during a basking session than at others. Walking (Fig. 1c) and turning in position (Fig. 6) followed a similar pattern, both occurring significantly more often than expected in the first 15 min of basking and disappearing in turtles basking in excess of 150 min. In both cases this was due to movements shortly following emergence. Animals would usually turn 90° after emerging and then walk a short distance. Extend legs (Fig. 1c) occurred more frequently than expected from 15 - 45 min and 120 - 135 min after emerging. Animals basking longer than 150 min extended their legs less frequently than expected. Unfortunately, nothing can be said about the data collected on head rubs and

kicks, etc. using the methods outlined above other than the high frequency for both in the fifth 15-min interval was due to the movements of a single female.

CHAPTER 4

DISCUSSION

Descriptions and patterns of basking behavior of chrysemid (*sensu* McDowell, 1964) turtles have been provided by only a few authors, notably Auth (1975), Boyer (1965), Litwin (1975), Lovich (1984), Moll and Legler (1971), and Zipko (1982). Qualitatively, basking behavior in *Pseudemys nelsoni* differs little from other species. Considering the overall morphological similarity among the species, it is not surprising that there are few, if any, differences in patterns of limb, head and tail movements. However, there are other ways basking behavior can differ, such as in quantity and quality of social interactions, responses to sun direction, and frequency of the various movements and postures common to these turtles. Since quantitative data on the nonsocial aspects of basking behavior are lacking in other published reports, comparisons with the basking behavior of *P. nelsoni*, described here, cannot be made. However, two authors (Auth, 1975; Litwin, 1975) have made qualitative assessments of basking behavior by devising temporal basking stages, permitting some comparisons with the data presented here.

Auth (1975) divides basking of *Trachemys scripta* into four stages, not including prebasking (arrival at the basking site). Litwin (1975) gives three stages for *Chrysemys picta*; prebasking, basking and post-basking. They are compared in Table 4. Other reports discussing details of the basking postures and movements generally support the descriptions given by Auth (1975) and Litwin (1975), but they also do not give quantitative information on these aspects of basking behavior. In fairness to these studies, their intent was not an analysis of basking postures and movements.

One might expect clear divisions if basking were divided into distinct stages, even if individual turtles entered them at somewhat variable times. For example, Auth (1975) considered stage 2 of basking to begin when animals first extended their legs. While legs were extended more frequently than expected in the 15 - 45 min interval, throughout the basking session animals changed postures repeatedly, extending and retracting their legs. Some animals never extended their legs during the basking session although other postures, such as a retracted head, suggested an advanced "stage" of basking by Auth's definition. Only turning and walking were clearly associated with a particular time period within the basking session, the first 15 min.

While the probability of a turtle performing a certain act or assuming a certain posture is related to the length of time the animal has been basking, the term "stage" implies temporally distinct units of behavior, each with a cohesive behavioral pattern or motif that is easily classified by an observer. The term "stage" also implies that one behavioral pattern is temporally dependent on another, as might be found in courtship. The only time during basking when some behaviors appeared dependent on previous ones was following emergence. Subsequent behavior patterns are probably best viewed as the result of interrelated variables, some correlated with basking time and some largely independent of basking time. In the former are rising body temperature and drying integument, in the latter, movements of surrounding turtles, wind, air temperature, sun direction, cloud cover, and the presence of insects. The data from the present study do not support the use of temporal "stages" as best characterizing the basking behavior of *P. nelsoni.*

Rather than attempt to explain variation observed in the behavior of basking turtles by the length of time they have been basking, the influence of environmental and social variables on postures and movements should first be explored. This approach has been helpful in other ethological studies. e.g., Ainley (1974) and Greenberg (1978).

Turtles that had been basking for longer times appeared more reluctant to enter the water when disturbed but data to examine this were not taken. Differential response to disturbance may also be explained by individual variation. More tolerant animals would be less likely to interrupt a basking session when disturbed, thus basking for longer periods of time than less tolerant animals.

LITERATURE CITED

Ainley, D.G. 1974. The comfort behaviour of Adelie and other penguins. Behaviour 50, 16-51.

Auth, D.L. 1975. Behavioral ecology of basking in the yellow- belled turtle, *Chrysemys scripta scripta* (Schoepff). Bull. Fla. State Museum Biol. Sci. 20, 1-45.

Bishop, Y.M.M., S.E. Fienberg, and P.W. Holland. 1975. Discrete Multivariate Analysis: Theory and Practice. MIT Press, Cambridge, Mass. 557 pp.

Boyer, D.R. 1965. Ecology of the basking habit in turtles. Ecology 46, 99-118.

Bury, R.B. and Wolfheim, J.H. 1973. Aggression in free-living pond turtles (*Clemmys marmorata*). Bioscience 23, 659-662.

Bury, R.B.J., J.H. Wolfheim, and R.A. Luckenbach. 1979. Agonistic behavior in free-living painted turtles (*Chrysemys picta bellii*). Biol. Behav. 1979, 227-239.

Chessman, B.C. 1987. Atmospheric and aquatic basking of the Australian freshwater turtle *Emydura macquarii* (Gray) (Testudines: Chelidae). Herpetologica 43, 301-306.

Crawford, K.M., J.R. Spotila, and E.A. Standora. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology 64, 989-999.

Greenberg, N. 1978. Thermoregulation aspects of behavior in the blue spiny lizard *Sceloporus cyanogenys* (Sauria, Iguanidae). Behaviour 59, 1-21.

Kramer, M. 1986. Field studies on a freshwater Florida turtle, *Pseudemys nelsoni*. *In* Drickamer, L.C. (ed.). Behavioral ecology and population biology. Privat, I.E.C., Toulouse. Pp. 29-34.

Litwin, S.C. 1975. Basking activity in the eastern painted turtle, *Chrysemys picta* picta. Master's Thesis, Rutgers Univeristy. 54 pp.

Lovich, J.E. 1984. An analysis of aggressive basking behavior in the eastern painted turtle. Master's Thesis, George Mason University. 79 pp.

McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London 143, 239-279.

Moll, E.O. and J.M. Legler. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. Bull. Los Angeles County Mus. Nat. Hist. Sci. 11, 1-102.

Rohlf, F.J. and R.R. Sokal. 1981. Statistical Tables, 2nd ed. W.H. Freeman and Co., N.Y. 219 pp.

SAS. 1983. SAS Institute, Inc. Cary, N.C.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry, 2nd ed. W.H. Freeman and Co., N.Y. 859 pp.

Spotila, J.R., R.E. Foley, J.P. Schubauer, R.D. Semlitsch, K.M. Crawford, E.A. Standora, and J.W. Gibbons. 1984. Opportunistic behavioral thermoregulation of turtles, *Pseudemys scripta*, in response to microclimatology of a nuclear reactor cooling reservoir. Herpetologica 40, 299- 308.

Sturbaum, B.A. 1982. Temperature regulation in turtles. Comp. Biochem. Physiol. 72A, 615-620.

Vogt, R.C. 1978. Systematics and ecology of the false map turtle complex, *Graptemys pseudogeographica*. Ph.D. Dissertation, University of Wisconsin, Madison. 375 pp.

Zipko, S.J. 1982. The basking behavior of painted turtles. Amer. Biol. Teacher 44, 406-412.

APPENDIX

TABLES AND FIGURES

Table 1. Definitions of basking behaviors of *Pseudemys nelsoni* treated in this study.

Behavior		Definition
MOVEMENTS		
Walk		Forward locomotion with the plastron either in contact with the substrate or elevated above it.
Turn		Orientation of the major body axis changes, usually 90° or 180°, without forward or backward locomotion.
Extend leg		The act of extending or stretching front or hind leg away from the body and then held in this position, at least momentarily. Although the leg may be touching the substrate it does not appear to be resting on it.
Head rub		Head is rubbed by the dorsal surface of one of the forefeet.
Kicks, etc.		Any repeated and/or rapid movement of the limbs, other than head rubs, which did not result in displacement or change in orientation. There was a continuous gradation from rubs to rapid kicks and shakes.
POSTURES		
Head		
	elevated	Neck mostly or completely extended, head held above level of carapace marginals.
	retracted	Neck flexed, more than half of head under carapace.
	other	Any intermediate position.
Front and Hind Legs		
	extended	Leg held extended or stretched away from the body, possibly touching the substrate but does not appear to be resting on it. Digits often spread or fanned.
	retracted	Leg flexed, more than half of foot under carapace.
	other	Any intermediate position, usually either on the substrate in a walking position or slightly retracted and touching or near the substrate but without resting on it.

Table 2. Probabilities of basking behaviors in a 15 min interval used in simulations to assess the validity of a G statistic for testing goodness-of-fit.

Behavior	Frequency	Probability	Frequency	Probability
Walks	0	0.8095	4	0.0003
	1	0.1201	5	0.0017
	2	0.0516	6	0.0020
	3	0.0138	7	0.0010
Turns	0	0.9167	3	0.0060
	1	0.625	4	0.0040
	2	0.0098	5	0.0010
Extend legs	0	0.7339	4	0.0052
	1	0.1881	5	0.0025
	2	0.0597	6	0.0015
	3	0.0091		
Head rubs	0	0.8883	8	0.0004
	1	0.0971	9	0.0003
	2	0.0016	10	0.0005
	3	0.0010	11	0.0005
	4	0.0010	12	0.0010
	5	0.0010	13	0.0011
	6	0.0010	14	0.0029
	7	0.0003	15	0.0020

Table 2. (continued)

Behavior	Frequency	Probability	Frequency	Probability
Kicks	0	0.7573	20	0.0012
	1	0.1339	21	0.0016
	2	0.0419	22	0.0003
	3	0.0119	23	0.0003
	4	0.0132	24	0.0005
	5	0.0018	25	0.0005
	6	0.0065	26	0.0005
	7	0.0042	27	0.0005
	8	0.0043	28	0.0005
	9	0.0041	29	0.0006
	10	0.0004	30	0.0005
	11	0.0005	31	0.0002
	12	0.0010	32	0.0010
	13	0.0007	33	0.0010
	14	0.0008	34	0.0005
	15	0.0006	35	0.0005
	16	0.0019	36	0.0005
	17	0.0024	37	0.0003
	18	0.0003	38	0.0002
	19	0.0003		

Table 3. Proportion of rejected null hypotheses from computer simulations assessing the robustness and power of the G statistic.

Behavior	sample size	H_0	H_1	H_2	H_3	H_4	H_5	H_6	H_7
Walks	4	0.000	0.005	0.014	0.029	0.027	0.045	0.059	0.058
	8	0.000	0.002	0.045	0.123	0.195	0.235	0.286	0.291
	16	0.000	0.012	0.175	0.500	0.663	0.744	0.811	0.820
	32	0.000	0.028	0.676	0.948	0.988	0.998	0.997	0.999
	64	0.001	0.159	0.988	1.000	1.000	1.000	1.000	1.000
Turns	4	0.000	0.000	0.000	0.002	0.003	0.013	0.016	0.018
	8	0.000	0.000	0.002	0.012	0.029	0.063	0.118	0.148
	16	0.000	0.000	0.010	0.074	0.227	0.375	0.544	0.621
	32	0.000	0.000	0.057	0.461	0.770	0.927	0.975	0.993
	64	0.000	0.000	0.399	0.946	0.997	1.000	1.000	1.000
Extend legs	4	0.000	0.000	0.000	0.012	0.011	0.007	0.012	0.018
	8	0.000	0.001	0.020	0.060	0.086	0.115	0.125	0.115
	16	0.000	0.003	0.154	0.368	0.510	0.585	0.611	0.637
	32	0.000	0.024	0.661	0.924	0.982	0.988	0.994	1.000
	64	0.000	0.177	0.995	1.000	1.000	1.000	1.000	1.000
Head rubs	4	0.233							
	8	0.174							
	16	0.169							
	32	0.177							
	64	0.161							
Kicks, etc.	4	0.580							
	8	0.753							
	16	0.898							
	32	0.964							
	64	0.969							

Note: Data were generated under the null and seven alternative hypotheses, the latter ranging from slight to moderate deviations from equal frequencies among the 10 15-min intervals (see Fig. 2 for examples).

Table 4. Comparison of the basking stages employed by Auth (1975) for *Trachemys scripta* and Litwin (1975) for *Chrysemys picta*.

Description	*C. picta*	*T. scripta*
Partial emergence, period of high alertness	Pre-bask (<1 - 5 min)	Stage 1A (<10 min, often bypassed by larger turtles)
Complete emergence	Pre-bask	Stage 1B
Stabilization of position	Basking, Period 1	Stage 1B
Orientation with respect to sun	----------	Stage 1B
Stretches/extends hind legs	Basking, Period 1	Stage 2
Limbs and head variable, generally less alert	Basking, Period 2	Stage 3
All limbs withdrawn, head usually withdrawn	Basking, Period 3 (rare)	Stage 3
Hyperactivity and moving about on basking site, concludes with animal returning to water	Post-bask	Stage 3
Basks in shade, may follow any other stage	----------	Stage 4

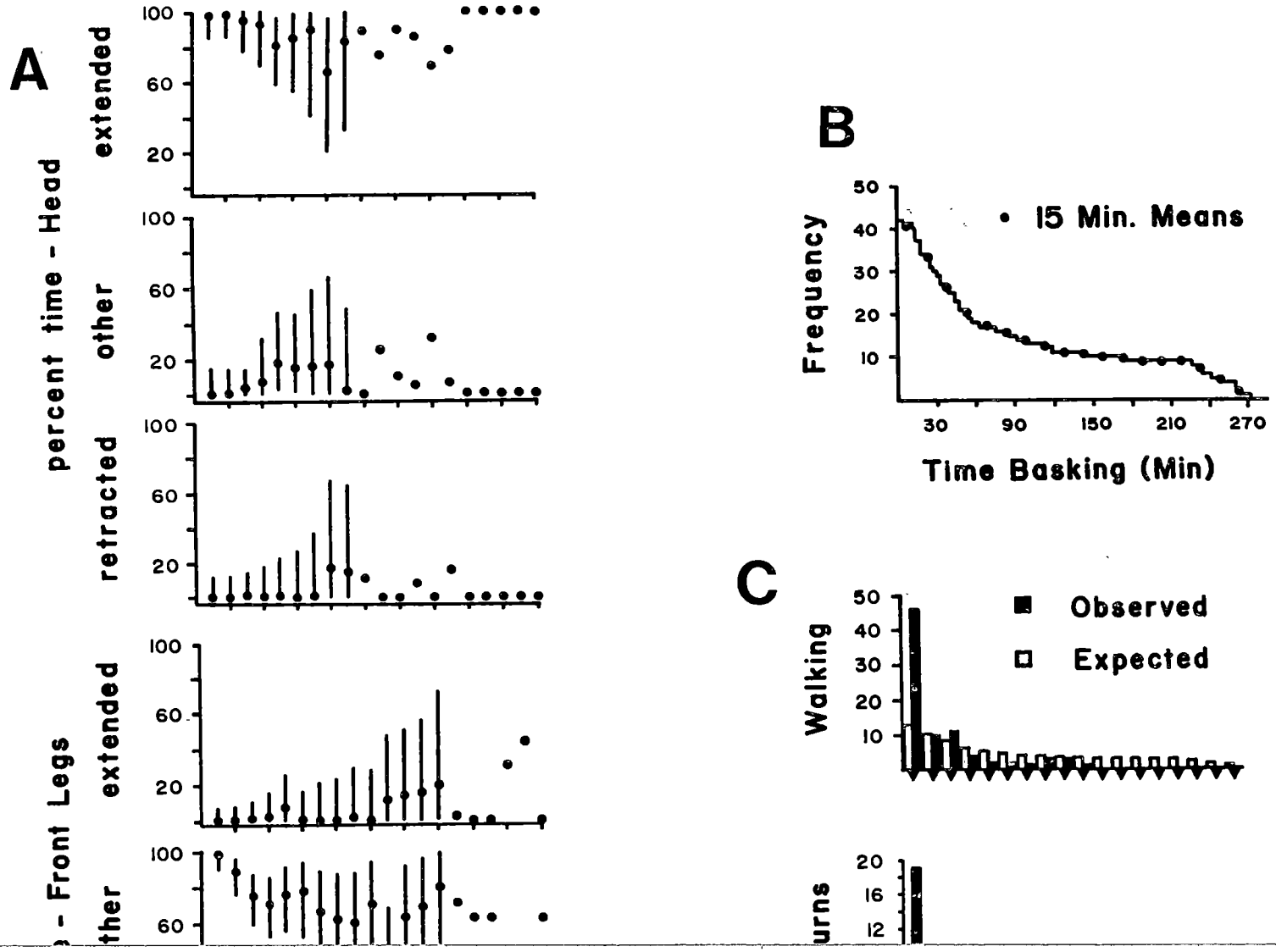
A
percent time - Head
extended
other
retracted
- Front Legs
extended
ther
100
60
20
B
Frequency
15 Min. Means
50
40
30
20
10
30
90
150
210
270
Time Basking (Min)
C
Walking
Observed
Expected
urns
20
16
12

Figure 2. Probabilities of the frequency of walking under three alternate hypotheses, from slight to moderate deviations from null hypotheses of equal frequencies among the 15 min intervals. The uppermost portion of each stacked column (open) is the probability of walking zero times (not visible in all columns). The filled portion below it is the probability of walking once, etc. The probabilities of walking five or more times are small for most columns and usually not visible.

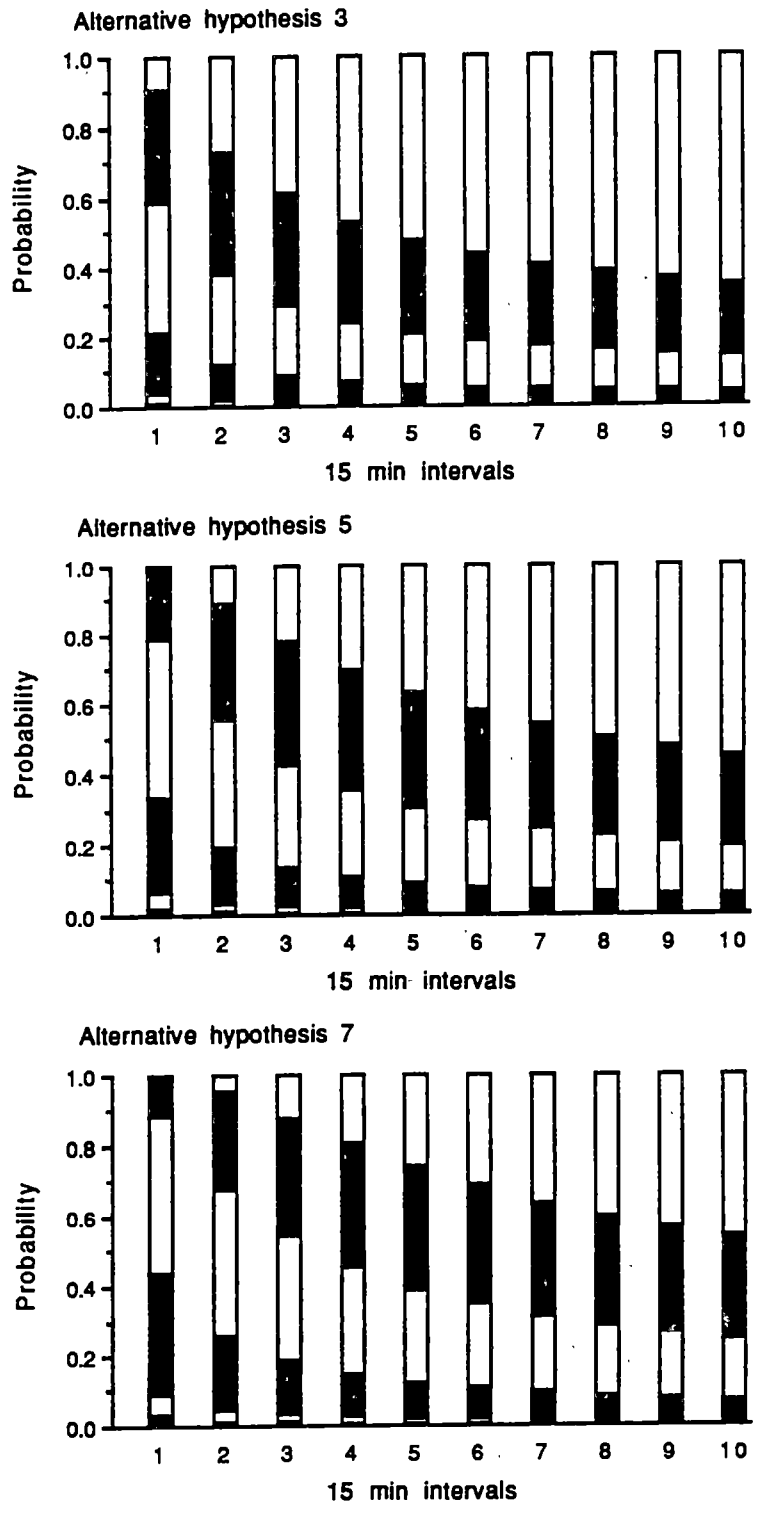
Alternative hypothesis 3
Probability
1.0
0.8
0.6
0.4
0.2
0.0
1 2 3 4 5 6 7 8 9 10
15 min intervals
Alternative hypothesis 5
Probability
1.0
0.8
0.6
0.4
0.2
0.0
1 2 3 4 5 6 7 8 9 10
15 min intervals
Alternative hypothesis 7
Probability
1.0
0.8
0.6
0.4
0.2
0.0
1 2 3 4 5 6 7 8 9 10
15 min intervals

Figure 2

PART 5

PRECOCIAL COURTSHIP IN *PSEUDEMYS* TURTLES

CHAPTER 1

INTRODUCTION

Precocial sexual behavior has been documented in mammals, birds and reptiles. For example, juvenile rats of both sexes may engage in mounting and thrusting (Hole and Einon, 1984) and Kruijt (1964) observed copulatory sitting and trampling in juvenile cockerels (*Gallus gallus*). In rats there is some evidence that precocial sexual behavior is correlated with circulating hormonal levels (Hole and Einon, 1984), suggesting that the neural substrate for sexual behavior exists prior to maturation. Precocial sexual behavior has also been observed in juvenile emydid turtles; in *Graptemys flavimaculata, G. kohni*, (Cagle, 1955), *Pseudemys concinna* (Cagle, 1955; Petranka and Phillippi, 1978), and *P. floridana* (Petranka and Phillippi, 1978). During those observations, an individual would rapidly vibrate the claws of its front feet (titillate) to other turtles or objects. In all five species, males use a similar display when courting females (Cagle, 1955; Vogt, 1978; Petranka and Phillippi, 1978; Part 2).

The adaptive value of precocial or juvenile "courtship" behavior, if any, is not clear. Hole and Einon (1984) were unable to demonstrate that animals prevented from precocial sexual behavior were at a sexual disadvantage when mature. Cagle (1955) suggested that juvenile turtles titillate to obtain information about the object or recipient, since he saw animals displaying only to novel objects and novel turtles. Petranka and Phillippi (1978) pointed out that the context and stereotypy of precocial courtship in turtles differ greatly from adult courtship.

The courtship display of male *Trachemys scripta elegans* appears to involve considerable time and energy (Jackson and Davis, 1972*a*). Indirect evidence, presented

below for *Pseudemys nelsoni*, indicates that precocial courtship behavior is also energetically costly. While the energy expenditure by adult males can be justified by tying it directly to reproductive success, it does not explain precocial courtship.

Here I describe precocial courtship in juvenile *P. nelsoni*, note ontogenetic changes, and give data on frequency and partner preferences. Some plausible hypotheses concerning the function of this behavior are presented. Fewer data were collected on this behavior in *P. floridana* and *P. concinna*; they are presented here to illustrate other points and permit species comparisons. In addition, Dale Jackson (in litt.) kindly made available to me his observations on these and additional species. For most of these observations, individual identities were not recorded. Thus, they are used only to supplement data on the expression of precocial courtship among different age classes and the postures used by different species. Finally, I discuss the numerous characteristics precocial courtship shares with some play behaviors.

CHAPTER 2

MATERIALS AND METHODS

Subjects

Observations were made on four *Pseudemys nelsoni*, three *P. floridana penninsularis*, and two *P. concinna suwanniensis*. In these species, two external characters are useful in distinguishing males from females; enlargement of the male's tail and hypertrophy of the male's foreclaws. The former became evident during the period of data collection. Relevant data concerning the history and size of these individuals is given in Table 1. During the 4 month study (Nov. 1984 - Apr. 1985) the animals were maintained in a 180 x 39 x 33 cm aquarium containing about 140 l of water on a 12L:12D cycle. Pieces of two cinder blocks provided hiding places and supported a rubber basking platform. Room temperature was maintained at 24 - 27°C. A 60 W light bulb suspended about 15 cm above the basking platform provided additional heat 8 h/day. The animals were fed to satiation at least three times/wk with live or frozen crickets, dog food and lettuce. A plaster-of-Paris block was placed in the water to provide supplementary calcium. The water was continuously filtered and completely replaced once/week.

Informal observations by Dale Jackson (in litt.) on precocial courtship in *Pseudemys nelsoni*, *P. alabamensis*, *P. floridana*, *P. concinna*, and *Trachemys scripta* were made from 1977 until 1989. Some of these animals were observed from hatching to age 12. They were maintained in various aquaria and a small plastic wading pool during this time.

Observation and Analysis Techniques

All interactions among turtles maintained in the laboratory at the University of Tennessee were noted using paper and pencil during 17 observation periods (810 min total). Observations usually began about one hour after feeding, in the afternoon, as informal observations suggested that interactions occurred at least as frequently or more so during this period and animals rarely basked at this time.

Animals usually avoided looking at each other when the anterior halves of both were closest and less than one body length apart (see Part 2). Therefore, I considered an interaction to begin when one turtle approached another while looking steadily at it, or when one turtle, already in the proximity of another, oriented to face it. Interactions that included approaches, or approaches and titillation are presented here.

Independently, data were gathered on the four *Pseudemys nelsoni* juveniles using focal animal sampling (Altmann, 1974) and checksheets (Hinde, 1973). Time periods were divided into 30 s intervals and the order of social and maintenance behaviors within these intervals was recorded. Focal animals for each session (30-60 min) were chosen at random. Observations on these turtles summed to 560 min. Data on frequency of vibration of the foreclaws were taken from several min of Super-8 film at 18 frames/s.

Statistical analyses were made using G-tests available on SPSSX (1986) or by hand calculations (Sokal and Rohlf, 1981).

CHAPTER 3

RESULTS

Description of Juvenile Courtship Behavior

During juvenile courtship, an individual repeatedly thrust its front limbs forward, rotating them inward (pronation) with the palms facing out, and rapidly vibrated the digits of its front feet. The display was clearly oriented toward the head of another individual. The rate of vibration of juvenile *P. nelsoni* (4.4 - 10.8 vibrations/s) does not differ from that of an adult male (7.0 - 16.0 vibrations/s), nor from three displays of a single *P. floridana* juvenile (5.0 - 6.7 vibrations/s)(Fig. 1). The behavior is as vigorous as in adult courtship.

Part of the energetic appearance of the behavior is due to the rapid vibration of the forefeet, but most is due to the continuous and, at times, brisk maneuvering of the displaying animal to maintain its position with respect to the recipient. The recipient was rarely still during displays, possibly as a consequence of them, which exacerbated the maneuvering requirements of the displaying individual.

The energetic cost of a display was not measured. However, oxygen consumption differences can be inferred from focal animal data by comparing the frequency that animals surfaced for air within 30 s after displaying with the frequency that they surfaced for air during other periods (excluding periods with displays) (Table 2). These results indicate that animals surfaced for air more frequently (G-test, $p = 0.025$) in the 30 s period following displays than they did during other 30 s periods.

On average, subjects displayed about once every 10 min in the focal animal sample. In the interactions data set, animals displayed on average once every 4 min. This does not adequately summarize precocial courtship frequencies because of the initial choice of observation periods (when interactions were numerous) and the clumped temporal distribution of this behavior. Generally displays occurred in bouts of one min or more. Clumping in time is demonstrated statistically by comparing the display frequency from the data using focal animal sampling in consecutive 5 min intervals with a Poisson distribution (Table 3).

Comparison with Adult Courtship Behavior

Precocial courtship behavior of juvenile *Pseudemys nelsoni* differs from adult courtship in several ways. The Initiation phase (Kramer and Fritz, 1989) is cursory or absent. This does not, however, imply that recipients are chosen at random (see below). Unlike adults, displays in juveniles occurred from two positions: 1) the displaying animal faced the recipient, within 45° of a direct line through their body axes (Fig. 2a), and 2) the displaying animal maneuvered above the recipient, both facing the same direction (Fig. 2b).

These two positions are typical of adult male courtship postures of some emydid turtles. The first is characteristic of *Chrysemys picta* (Taylor, 1933), and some *Trachemys* (Jackson and Davis, 1972*a*) and *Graptemys* (Vogt, 1978); the second of *Pseudemys* species in which courtship has been observed (Marchand, 1944; Jackson and Davis, 1972*b*; Part 2). While positions were not recorded during observations, of 30 juvenile *P. nelsoni* displays filmed from this period, all but two were head-to-head. Data collected by D. Jackson (in litt.) on *P. nelsoni* corroborates the use of both positions, each position used about half the time by his juveniles.

Mounts rarely followed displays. After one or more bouts, the displayer would usually abandon the recipient. While mounts are not common in adult *Pseudemys nelsoni* courtship behavior (Kramer and Fritz, 1989), only two were seen in these juveniles during the entire period that they were under observation.

Unlike adults, where females rarely display, juvenile females displayed frequently (Fig. 3). A G-test showed significant differences in the number of displays among the four juveniles, three of which were female, however the number of displays by the male (51) was closest to the mean (52.5).

Other differences include the following. Juveniles displayed only to others on the substrate, whether moving or stationary. Males in the field displayed only to swimming females (Kramer and Fritz, 1989). On occasion, the interaction between two juveniles attracted a third, who started displaying to one of the other two. On one occasion all four juveniles were clustered together, with at least three displaying. Adults were not seen to join courting pairs in the field.

Responses to Juvenile Courtship

The response to the displays varied, although not in a systematic way. Most often the recipient appeared to ignore the displaying individual. Less often the recipient appeared to be disturbed by the display and turned away or left (Fig. 3). On several occasions the recipient gaped, snapped at, or bit an especially persistent displaying individual. This behavior invariably halted further or incipient displays and this recipient would not be approached by the displaying animal again for several minutes. In general, the individuals reacted similarly regardless of the displayer's identity except for one female juvenile (#3),

who turned away or left very frequently after being displayed to by the male (#2) (see also Part 3).

Ontogeny of Juvenile Courtship Behavior

The youngest displaying *Pseudemys nelsoni* I observed was wild-caught and about five months old. It displayed briefly to a piece of dried dog food in the water before biting it. Cagle (1955) observed a much younger (35 day old) *Pseudemys concinna suwanniensis* displaying to a snail before eating it. One of the laboratory reared *P. nelsoni* in this study displayed to a live cricket before eating it when about one year old. D. Jackson (in litt.) observed many instances of precocial courtship in young *P. nelsoni*, *P. alabamensis*, *P. concinna*, and *T. scripta*, starting from three weeks of age.

Species Differences and Discrimination

Precocial titillation was much more frequent in *Pseudemys nelsoni* juveniles than in the other two species (Table 4). However, the total number of displays for each species was accurately predicted when the total number of approaches of each species is included as a covariate (G-test, $p = 0.997$, Table 4). Thus, the large differences in display frequency can be attributed to differing rates of social interactions among juveniles of the three species.

Sufficient displays were performed by *Pseudemys nelsoni* juveniles to determine if displays were equally likely to be given to con- and heterospecifics. *P. nelsoni* juveniles display significantly more to conspecifics (210 vs. 3, G-test, $p < 0.001$). This suggests that displaying juvenile *P. nelsoni* can and do discriminate between con- and

heterospecifics and preferentially display to conspecifics. Insufficient displays were given by individuals of the other two species during data collection for statistical treatment.

Partner Preferences of Individual *Pseudemys nelsoni*

The partner preferences of the four juvenile *Pseudemys nelsoni* were examined. There are significant differences among the total number of displays given by each animal (G-test, $p < 0.01$) and the total number of displays received by each animal ($p < 0.01$)(Fig. 3). Furthermore, these factors are not independent ($p < 0.01$); knowing the total number of displays given by each individual and the total number of displays received by each of the recipients is not a good predictor of the number of displays that any one individual gives to another. The model of independence was a good predictor of only two of the subjects' display behavior, indicating that recipients are not chosen at random.

The display behavior of each juvenile was therefore examined separately. All four juveniles were selective in their choice of recipients (G-test, all $p < 0.01$). Two of the juvenile females directed most of their displays to the juvenile male (Fig. 3).

There is a strong relationship between approaching an individual and displaying to it; a regression of these individuals' displays on their approaches yielded a coefficient of determination (r^2) of 0.69 (Fig. 4). That juveniles selectively approach preferred recipients suggests that they can distinguish among potential conspecific recipients before displaying.

CHAPTER 4

CONCLUSIONS

Evolution of Courtship in *Pseudemys*

Based on the literature reviewed above and the data presented here I suggest that the Swim Above position taken by adult male *Pseudemys* during courtship derives from the head-to-head position found in related emydid turtles. The Swim Above position is restricted to the genus *Pseudemys* while the head-to-head position is used by at least three genera of emydid turtles for titillation. While ontogeny may not always parallel phylogeny (Gould, 1977), juveniles in the four species of *Pseudemys* turtles for which data is available were all seen to display from the head-to-head position. No instances of the Swim Above position have been reported by any juvenile exhibiting precocial courtship in species where adult males use the head-to-head position.

Function of Precocial Courtship in *Pseudemys*

While different in some aspects from the courtship behavior of adult male *Pseudemys nelsoni* (Kramer and Fritz, 1989), juvenile courtship behavior shares most of its components with adult courtship and not with other adult or juvenile behaviors. In particular, juvenile courtship resembles the Swim Above phase (Kramer and Fritz, 1989) of adult courtship. The one instance of an adult female displaying in the literature (Jackson, 1977) was more similar to juveniles' displays than those of adult males because

this female also displayed from the head-to-head position. Displays by females were not observed by Kramer and Fritz (1989) in captivity or in the field.

Since the animals from this study demonstrated high selectivity of partner choice prior to displaying, it is unlikely that the titillation display by either sex serves a species or sex recognition function, as suggested by Jackson and Davis (1972*a*), in juveniles or adults (see also Part 2). If adult males use this display to induce female receptivity, its presence in juveniles is paradoxical. Yet, the high frequency of these apparently costly displays suggests that this behavior should have an obvious function. I speculate below on several functions I consider to be the most likely candidates to explain precocial courtship in turtles and comment on the degree to which these data support each.

1) Maturation

If adult courtship was properly expressed only after an inflexible ontogeny (i.e., complete expression of adult courtship occurs only if precursor courtship patterns were expressed at specific times during development), juveniles might exhibit precocial courtship even if it were slightly maladaptive. In this case, the form of the behavior expressed by juveniles might differ considerably from adult courtship behavior without adverse consequences on its final form. In fact, the behavior does differ (see above) in some respects from adult male courtship behavior. However, this explanation is inadequate in other ways. First, the display is performed very frequently. One might suppose that this behavior would be infrequently performed, since it appears energetically costly, may attract predators, and may not have realized benefits for juveniles. Second, the titillating component, which would presumably be the behavior requiring maturation, does not appear to differ in juveniles and adults, nor does it "improve" with age, having all the

ingredients of a "fixed" action pattern (Schleidt, 1974). Third, this function would not explain why female juveniles perform the display.

2) Practice to acquire social skills

There may be important social skills that must be learned for males to become reproductively successful. Successful courtship by males may require a delicate adjustment of the courtship display to particular individuals, situations or seasons rather than through stoic persistence. Those turtles that have been unable to participate in precocial courtship with others may be poor predictors of their partner's movements, give inappropriate responses or displays, or may not learn the optimal orientation from which to give the display. It may be advantageous for them to start when young so as to be better prepared when sexual maturity is attained.

There is evidence that the stimulus control for this behavior shifts with age. The youngest animals display to many small objects while older juveniles and adults display mostly to conspecifics. The high frequency of this behavior among juvenile *P. nelsoni* allows each individual to have many interactions with others, providing substantial opportunities for learning to occur. This explanation, however, fails to account for display behavior in juvenile females, nor does it explain partner preferences. Although natural observations of adults are clearly deficient, there is nothing to suggest that this display is used in contexts other than courtship in nature. The function of the display by the adult female in Jackson's (1977) study remains unclear.

3) Artifact of captivity

Bizarre behaviors, clearly artifacts of long-term captivity, are exhibited by many animals (Heideger, 1964) although this has not been well documented in reptiles. If the behavior is not aberrant it may be abnormal in other respects, e.g., occurring more or less frequently than in nature. The juveniles used in this study did not have to forage or travel appreciable distances to bask. Density (i.e., crowding) in the water probably exceeded natural levels by several orders of magnitude. Animals may have had difficulty escaping the attention of others since they could not leave the aquarium.

The possibility that precocial courtship is an artifact of captive conditions cannot be addressed by these data. Juvenile *Pseudemys nelsoni* were rarely observed in the field. Thus, the frequency and nature of naturally occurring interactions are unknown. However, it is unlikely that individuals in the lab exhibited aberrant behavior because they could not avoid other turtles. An animal appearing to avoid another usually did not swim away, crawl into a hiding place or retract into the shell. Instead it would turn or crawl several cm, then resume the behavior interrupted by the displayer. Further aggressive behavior (gapes, snaps and bites) was infrequent and invariably halted displays and approaches. Finally, precocial courtship displays were observed by wild caught *P. nelsoni*, *P. floridana*, and *P. concinna* during informal observations as well as by captive reared *P. nelsoni* (see above).

Precocial Courtship and Play

It is clear that the data do not support any of the above proposed functions with great confidence. Precocial courtship in turtles does not seem to have an obvious function. This section will discuss the similarities of precocial courtship in *Pseudemys nelsoni* with play

behavior, for which demonstrable functions have also proved elusive. Two of the explanations given above, i.e., maturation and practice, have been proposed, among others, as possible functions of play (Fagen, 1981).

Play has been a difficult behavior to define. The definition given by Bekoff and Byers (1981) is clear and consistent with most others, "*Play* is all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing" (p. 300). Fagen (1981) reviewed the characteristics of play behavior and extracted the least disputed examples (p. 44). His list (Table 5) is augmented by two others, which give the general characteristics of the structure and causation of play (p. 45 - 46). Some items on these latter lists, as Fagen states, are controversial. However, they give some basis by which to judge the plausibility of play or play-like behavior as a possible explanation for precocial courtship behavior in turtles. The main characteristics of play are compared with precocial courtship in turtles below and in Table 5.

The first characteristic, that behaviors occurring in play are similar, but not identical, to those occurring in a well- defined functional context of adults (or juveniles), clearly applies to precocial courtship in these turtles. For example, the orientation, maneuvering and titillating behaviors observed during precocial courtship of juvenile *Pseudemys nelsoni* are similar, but not identical, to adult male courtship. The second, that behaviors in play are exaggerated, is difficult to assess with the data collected. The individual motor patterns do not appear to differ from those of adults in the way that the motor patterns of young mammals playing are exaggerated when compared to those motor patterns in 'serious' contexts. There may be differences between adult and precocial courtship in the duration or timing of the various behavioral acts; for the most part, these were not measured. The duration of a bout of titillation does appear, on average, somewhat longer (exaggerated?) in

juveniles than in the single adult male measured (Fig. 1). The third characteristic, that "...individual acts are repeated more often in play sequences" (p. 44) is also difficult to assess because the data needed to make detailed comparisons between precocial and adult courtship have not yet been collected.

There remain two characteristics that may be less representative of play behavior, that play sequences tend to be variable and that they lack the normal consummatory behavior and biological consequences of non-play behavior. Precocial courtship behavior of these turtles, as described above, appears to possess both attributes.

In most mammals, 1 to 10% of the total time budget is spent in play. This is time and energy that could conceivably be put to other uses, e.g., growth or foraging (Fagen, 1981). From focal animal sampling in this study an individual displayed about once every 10 min. In the data set when interactions alone were recorded, individuals displayed about once every 4 min. This suggests that the amount of time occupied by this behavior is within the range of that occupied by mammals at play. Properly maintained captive animals often play more than wild ones (Fagen, 1981; Burghardt, 1988). The high frequency of precocial courtship exhibited by juvenile *Pseudemys nelsoni* may result from captivity, paralleling play.

Play has traditionally been thought to be virtually non- existent in reptiles (Burghardt, 1984). There are several reasons for this, including: 1) reptiles do not appear to possess the physiological scope to engage in vigorous play activity, 2) most reptiles lack parental care leaving neonates without a food supply or protection, and 3) reptiles are not capable of changing their facial expression so that indicators of play (to humans), such as the 'play face' typical of canid or primate play, are not evident. This last point has also made it difficult to distinguish play in birds from other behaviors (see also Ficken, 1977). Burghardt (1988) discusses why reptile life history traits tend to exclude play.

That play may be too energetically costly to a reptile is contradicted by the data presented above as apparently functionless and vigorous behavior is engaged in with great frequency. While most reptiles may not be capable of large increases in basal metabolic rate, *Trachemys scripta*, a related species, is capable of aerobically supporting a 24 fold increase in basal metabolic rate at 30°C, comparable to that of active lizard species (Gatten, 1974). Furthermore, the aquatic medium allows locomotion and maneuvering at a far lower energetic cost than similar behaviors on land (Schmidt-Nielsen, 1972).

There are several reasons that turtles (some of these may apply to crocodilians) might be expected to be the most likely reptile to have evolved play or play-like behavior. Many turtles are aquatic, thus costs of locomotion are low. They are tolerant of conspecifics and are often found in aggregations (Bury, 1979) allowing ample opportunity for interactions to occur. The social system of *P. nelsoni* and perhaps others appears complex (Kramer, 1986) and may be mediated through individual recognition (Part 6). Turtles are considered to be "intelligent", evident by the consistent bias of comparative psychologists to use them rather than other reptiles. About 50% of the studies cited by Burghardt (1977) in his review of the reptilian learning literature used Chelonians. Finally, turtles are long lived which would give any of the proposed long range benefits (see Fagen, 1981) sufficient time to accrue.

Overall, the results reported here are consistent with the hypothesis that play, perhaps a primitive form of it, explains precocial courtship behavior in juvenile *P. nelsoni*. As untidy as it may seem, if this behavior is primitive play, not finding an obvious benefit for it is not surprising, nor is the performance of it by both sexes.

LITERATURE CITED

Altmann, J. 1974. Observational study of behaviour: Sampling methods. Behaviour 49, 227-267.

Bekoff, M. and J.A. Byers. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: An ethological hornet's nest. *In* Immelmann, K., G. Barlow, M. Main and L. Petrinovich (Eds.). Issues in behavioral development: The Bielefeld interdisciplinary conference. Cambridge Univ. Press, N.Y. Pp. 296-337.

Burghardt, G.M. 1977. Learning processes in reptiles. *In* Gans, C. and D. Tinkle (Eds.). The Biology of the Reptilia, vol. 7. Academic Press, N.Y. Pp. 555-681.

Burghardt, G.M. 1984. On the origins of play. *In* Smith, P.K. (Ed.). Play in Animals and Humans. Basil Blackwell Publ. Ltd., N.Y. Pp. 5-41.

Burghardt, G.M. 1988. Precocity, play, and the ectotherm- endotherm transition: Profound reorganization or superficial adaptation? *In* Blass, E.M. (Ed.). Handbook of behavioral neurobiology, vol. 9. Developmental psychobiology and behavioral ecology. Plenum Press, N.Y. Pp. 107-148.

Bury, R.B. 1979. Population ecology of freshwater turtles. *In* Harless, M. and H. Morlock (Eds.). Turtles: Perspectives and research. John Wiley and Sons, N.Y.

Cagle, F.R. 1955. Courtship behavior in juvenile turtles. Copeia 1955, 307.

Fagen, R. 1981. Animal Play Behavior. Oxford University Press, Inc., N.Y. 684 pp.

Gatten, R.E., Jr. 1974. Effects of temperature and activity on aerobic and anaerobic metabolism and heart rate in the turtles *Pseudemys scripta* and *Terrapene ornata.* Comp. Biochem. Physiol. 48A, 619-648.

Gould, S.J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Mass. 501 pp.

Ficken, M.S. 1977. Avian play. Auk 94, 573-582.

Hinde, R.A. 1973. On the design of check-sheets. Primates 14(4), 393-406.

Hole, G.J. and D.F. Einon. 1984. Play in rodents. *In* Smith, P.K. (Ed.). Play in Animals and Humans. Basil Blackwell Publ. Ltd., N.Y. Pp. 95-117.

Jackson, C.G. 1977. Courtship observations on *Chrysemys nelsoni* (Reptilia, Testudines, Testudinidae). J. Herpetol. 11(2), 221-222.

Jackson, C.G., Jr. and J.D. Davis. 1972*a*. A quantitative study of the courtship display of the red-eared turtle, *Chrysemys scripta elegans* (Wied). Herpetologica 28, 58-64.

Jackson, C.G., Jr. and J.D. Davis. 1972*b*. Courtship display behavior of *Chrysemys concinna suwanniensis*. Copeia 1972, 385-387.

Kramer, M. 1986. Field studies on a freshwater Florida turtle, *Pseudemys nelsoni*. *In* Drickamer, L.C. (Ed.). Behavioral ecology and population biology. Privat, I.E.C. Toulouse. Pp. 29-34.

Kramer, M. and U. Fritz. 1989 Courtship behavior of the turtle, *Pseudemys nelsoni*. J. Herpetol. 23, 84-86.

Kruijt, J.P. 1964. Ontogeny of social behaviour in Burmese red jungle fowl (*Gallus gallus spadiceus*). Behaviour Suppl. 12, 1-201.

Marchand,L.J. 1944. Notes on the courtship of a Florida terrapin. Copeia 1944, 191-192.

Petranka, J.W. and A. Phillippi. 1978. Observations on the courtship behavior of juvenile *Chrysemys concinna concinna* and *Chrysemys floridana hoyi* (Reptilia, Testudines, Emydidae). J. Herpetol. 12(3), 417-419.

Schleidt, W.M. 1974. How "fixed" is the fixed action pattern? Z. Tierpsychol. 36, 184-211.

Schmidt-Nielsen, K. 1972. Locomotion: Energy cost of swimming, flying, and running. Science 177, 222-228.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry, 2nd ed. W.H. Freeman and Co., N.Y. 859 pp.

SPSSX User's Guide, 2nd ed. 1986. McGraw-Hill, N.Y. 988 pp.

Taylor, E.H. 1933. Observations on the courtship of turtles. Univ. of Kansas Sci. Bull. 21, 269-271.

Vogt, R.C. 1978. Systematics and ecology of the false map turtle complex *Graptemys pseudogeographica*. Ph.D. dissertation, Univ. of Wisconsin, Madison. 375 pp.

APPENDIX

TABLES AND FIGURES

Table 1. History and size of subjects; *Pseudemys nelsoni*, *P. floridana* and *P. concinna*.

ID	Species	Procurement	Measurements (8 April 1985) plastron length (mm)	mass (g)
1	*P. nelsoni*	captive reared hatched Aug. 1982	133	491
2	*P. nelsoni*	captive reared hatched Aug. 1982	131	460
3	*P. nelsoni*	captive reared hatched Aug. 1982	109	298
4	*P. nelsoni*	captive reared hatched Aug. 1982	140	532
6	*P. concinna*	captured July 1983 Luraville, Fla.	131	446
7	*P. concinna*	captured July 1983 Luraville, Fla.	98	214
8	*P. floridana*	captured July 1984 Apopka, Fla.	83	141
9	*P. floridana*	captured July 1984 Apopka, Fla.	61	63
10	*P. floridana*	captured July 1984 Apopka, Fla.	102	236

Table 2. Breathing frequency.

Time interval	Frequency of surfacing	
	zero	one or more
within 30 s of displaying	8	15
other 30 s intervals	617	442

Note: Frequency that juvenile *Pseudemys nelsoni* surfaced to breathe in 30 s intervals, excluding those in which they displayed ($p = 0.25$, G-test).

Table 3. Display frequency.

number of displays/5 min	Frequency of 5 min periods	
	observed	expected
0	93	59.95
1	6	37.47
2	6	11.71
3 or more	7	2.87

Note: Comparison of display frequency in 5 min periods of juvenile *Pseudemys nelsoni* with expected frequencies from a Poisson distribution demonstrating that displays occurred in bouts ($p < 0.01$, G-test).

Table 4. Total frequency of displays and approaches of each species (*Pseudemys nelsoni*, *P. floridana* and *P. concinna*).

Species	# of individuals	# of approaches	# of displays
P. nelsoni	4	449	213
P. floridana	3	21	1
P. concinna	2	76	2

Note: Results of G-tests indicate that, if data of all individuals within each species are combined, approach frequency is a good indicator of display frequency ($p = 0.997$, 1 d.f., including number of approaches as a covariate; $p < 0.001$, 2 d.f., without approaches).

Table 5. A comparison of precocial courtship behavior of *Pseudemys nelsoni* with play behavior characteristics (from Fagen, 1981, pp. 45-46).

Found in precocial courtship	Not found in precocial courtship
Structure	
Play acts having temporal structure may be relatively incomplete...	Acts that involve several parts of the body or may lack some components found in nonplay...
Play sequences are relatively brief.	
Play sequences may be relatively reordered or disrupted.	
Play sequences show relatively rapid alternation of acts.	
Play sequences are relatively incomplete.	
Causation	
Play sequences may be interrupted by higher-priority behavior and fragmented by inclusion of motivationally irrelevant activities.	Play appears to be pleasurable to to the performers.†
Play occurs in a relaxed motivational field.	Play patterns are relatively inhibited.
Non-specific items, including objects and living or dead organisms, may substitute for a conspecific partner in play.	There is a specific motivation to play.†
Transitions from play to nonplay, or mixed forms of play may occur.	

Table 5. (continued)

Found in precocial courtship	Not found in precocial courtship
Play occurs characteristically in immature animals.	
Play sequences occur in different situations from nonplay sequences that include the same acts, or they occur as a result of different stimuli, including stimuli normally inadequate to elicit these acts.	
In a given play sequence, the same behavior may be directed in turn at different stimuli.	
The patterns of behavior in play is relatively less dependent on normal stimulus-response relationships.	
In play, animals return repeatedly to the same stimulus source.	

†Could not be ascertained.

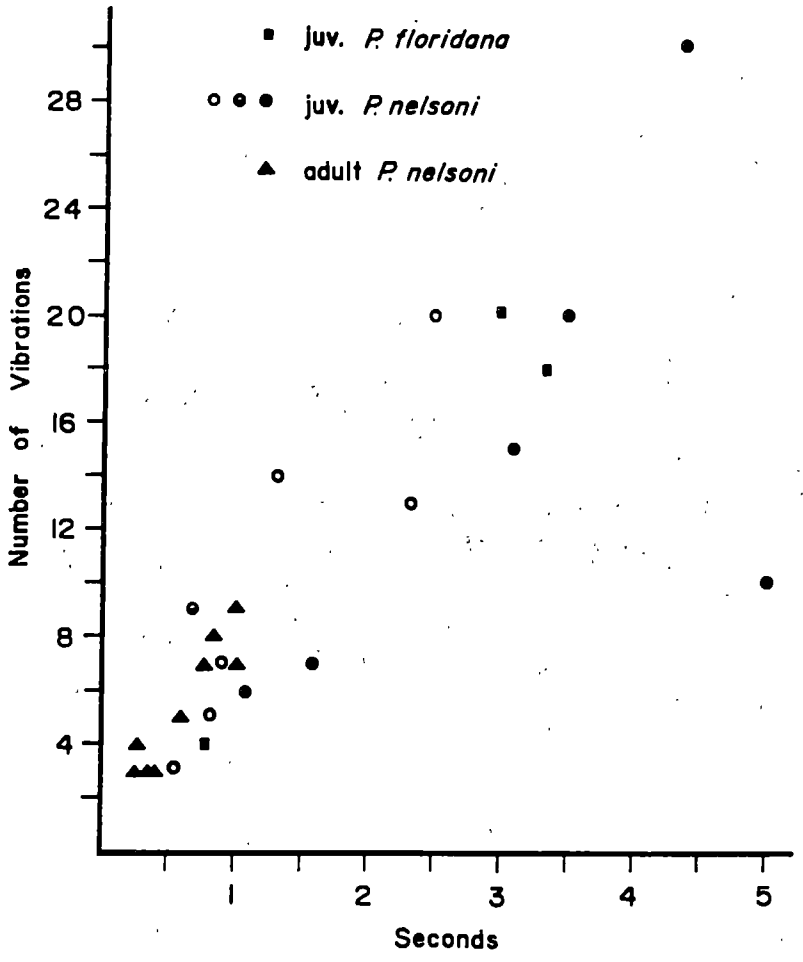

Figure 1. Frequency of claw vibrations in a display vs. time (s) of *Pseudemys nelsoni* and *P. floridana*. Three different juvenile *P. nelsoni* are represented by circles (open, filled, half filled). The triangles are data from a single *P. nelsoni* male and the squares a single juvenile *P. floridana*. The outlier (lower right) is probably from two contiguous displays.

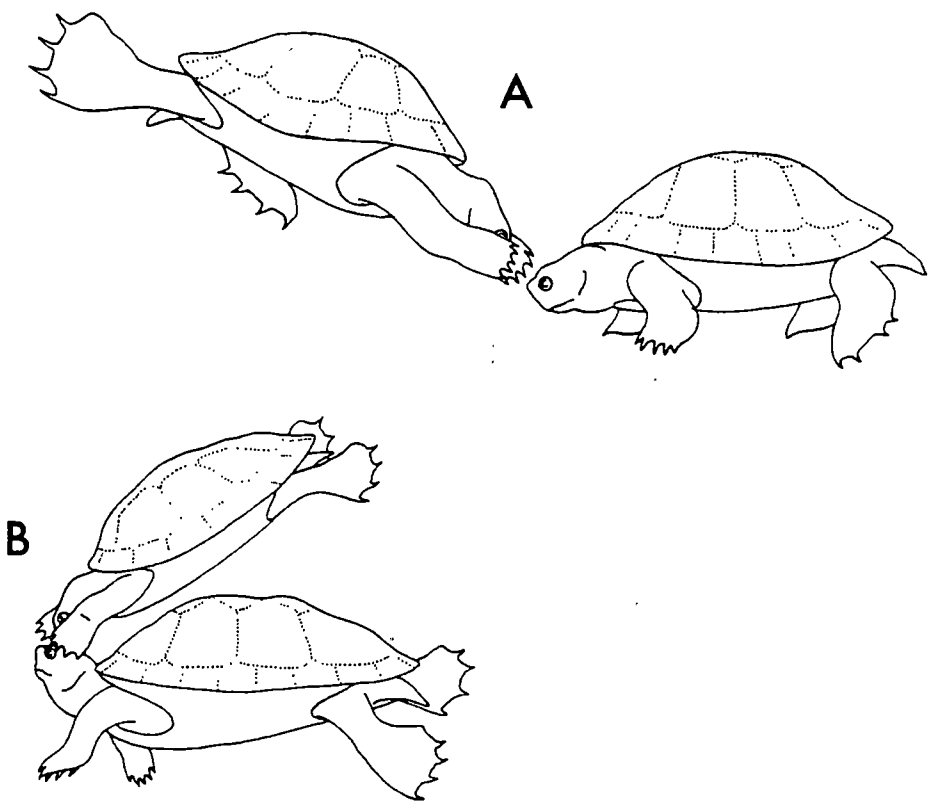

Figure 2. Positions of displaying juvenile *Pseudemys nelsoni*. A) Head-to-head (characteristic of *Trachemys scripta elegans*), B) Swim above (characteristic of adult *Pseudemys*).

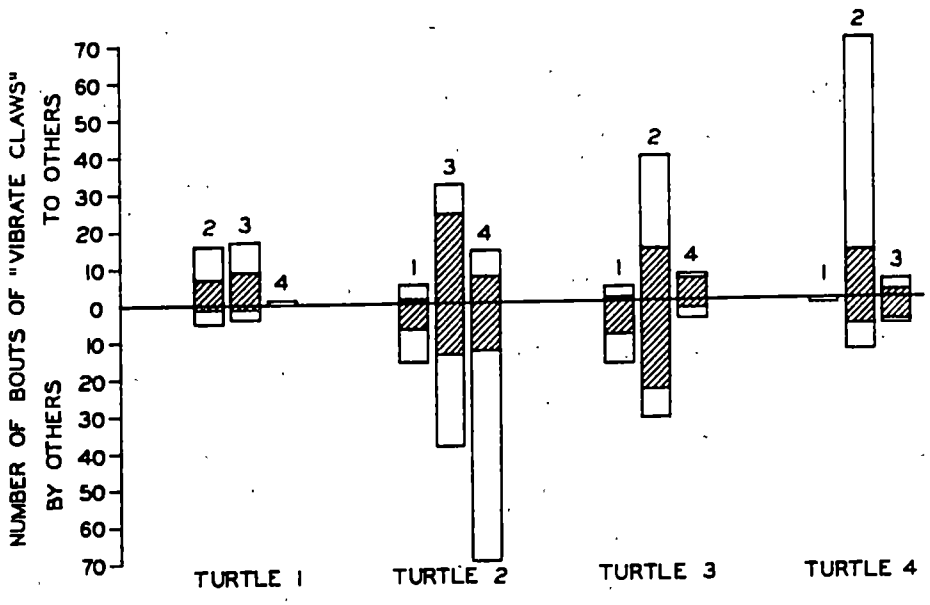

Figure 3. Display frequencies of each *Pseudemys nelsoni* juvenile to each of the other *P. nelsoni*. Above the bar are the display frequencies to others (with their identifying number). Below the bar are the same data rearranged for each juvenile as a recipient of others' displays. The hatched portions of each bar give the frequencies that the recipient turned away or left. Turtle 2 was a male, the others female.

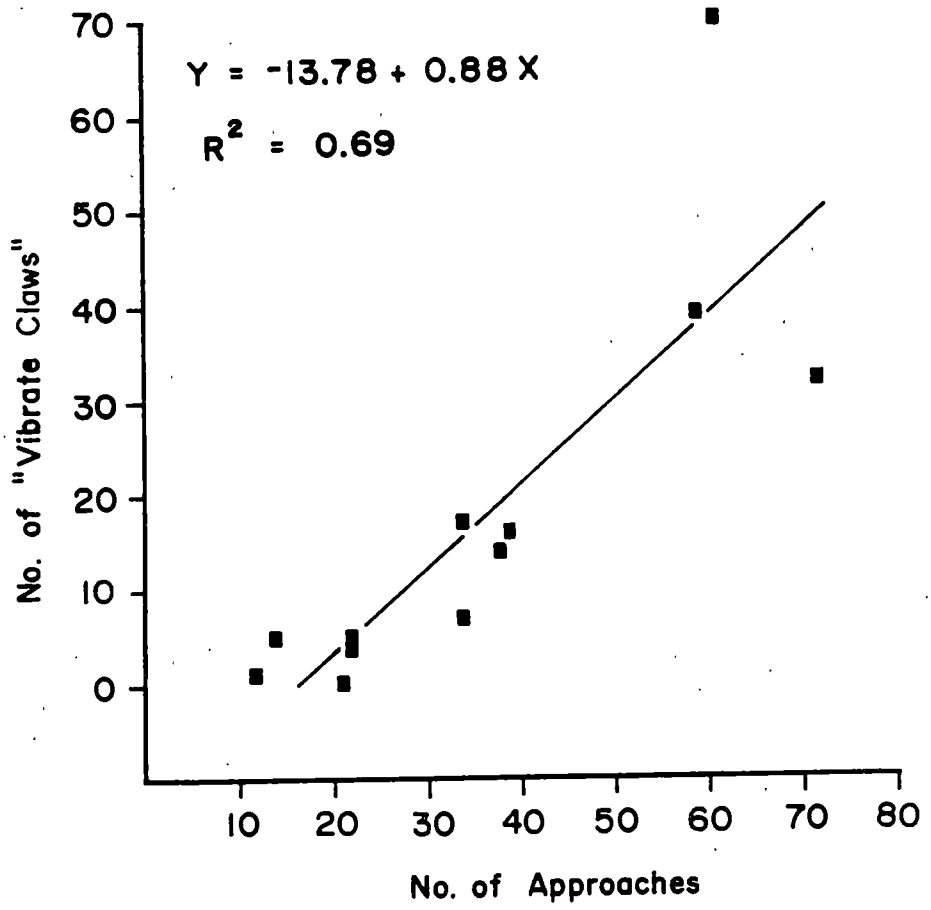

Figure 4. Approaches and titillation. The number of titillation bouts as a function of the number of approaches of each subject to each of the others (*P. nelsoni* juveniles only).

PART 6

INDIVIDUAL DISCRIMINATION IN *PSEUDEMYS* TURTLES

CHAPTER 1

INTRODUCTION

Individual recognition has been experimentally demonstrated in some mammals, birds, fish, invertebrates (reviewed in Colgan, 1983; Johnson, 1977), and the lizard, *Dipsosaurus dorsalis* (Glinski and Krekorian, 1985). Other lizard studies suggest individual discrimination abilities, although this was not always the study's objective (e.g., Andrews, 1985; Crews, 1975; Dugan, 1982; Ferguson, 1971; McDonald, 1987). Perhaps the first to discuss the importance of researching individual and species discrimination in turtles was Casteel (1911). Rather than use individual turtles as stimuli, however, he used more standard tests of visual acuity and form discrimination, one of the first of many such inquiries (reviewed in Burghardt, 1977).

Laboratory studies by Evans et al. (1973, 1974) on the turtle, *Trachemys scripta*, suggest individual discrimination abilities. Their objective was to demonstrate that two juveniles could be "imprinted" on each other. Subjects were tested after several months of cohabitation or receiving water samples from the other turtle's living quarters. Familiar conspecifics were found significantly more often in close physical proximity than were pairs of strangers.

A social system based on dominance hierarchies is often taken as evidence that the species possesses individual recognition capabilities, although dominance hierarchies may also be based on single characters, e.g., size (McBride, 1964; Colgan, 1983). Field observations suggesting dominance hierarchies in chrysemid (*sensu* McDowell, 1964, hereafter, chrysemid) turtles have been reported in many basking studies (Auth, 1975; Lovich, 1984; Bury et al., 1979) and from observations of animals in the water in

Trachemys scripta (Lardie, 1983) and *Pseudemys nelsoni* (Kramer, 1986). Harless (1979) speculates that most species of turtles form dominance hierarchies in nature.

In captive chrysemid turtles, dominance hierarchies were seen in *Trachemys scripta* (Evans, 1952; Lardie, 1983), *Chrysemys picta* (Evans, 1940), and a group of *Pseudemys nelsoni*, *P. floridana*, and *P. concinna* juveniles (Kramer, unpubl. data). Additional behavioral data on this latter group suggests individual discrimination; the juveniles demonstrated significant preferences when approaching and exhibiting precocial courtship to others (see Part 5).

In many species, dominance hierarchies are established by intensive fighting. Later, to reinforce dominance relationships, brief agonistic encounters unlikely to lead to injury ("squabbling"), may occur (McBride, 1964). The male-male interactions in *Pseudemys nelsoni* described by Kramer (1986, Part 2) are probably best labeled as "squabbling". They are composed of short bouts which include gaping (interpreted as threats) and retraction into the shell; pushing, bites and chases are infrequent. These encounters often do not yield clear winners and losers. After an agonistic interaction the animals frequently remain in close proximity without further aggressive behavior.

Individual recognition in *Pseudemys nelsoni* is also suggested by male-female aggressive interactions, in which the male chases a female, bites her on the forelimb, and drags her to the bottom. He pulls vigorously on her forelimb in short bouts for up to one-half hour before releasing her. One possible interpretation of this behavior is that females use information from these interactions to later select mates, perhaps by using male vigor as an indicator of genetic merit (Kramer, 1986). Individuals in this population appeared to be fairly sedentary (Kramer, 1986; Part 7) and thus would be expected to encounter the same individuals repeatedly.

In the experiments described below I tested for the ability of individual *Pseudemys nelsoni* and *P. floridana* to distinguish between two turtles, both either conspecific or heterospecific with the subject. Both species were used because interspecific interactions involving *P. nelsoni* and *P. floridana* were occasionally seen during underwater observations at Rock Springs run, Apopka, Fla. (see Part 2). *Sternotherus odoratus* and *Trionyx ferox*, the other abundant turtle species at this site, were not included because no interactions were observed involving either of these species with *P. nelsoni* or *P. floridana*.

CHAPTER 2

EXPERIMENT 1

Introduction

The many studies of discrimination and learning abilities of turtles, reviewed by Burghardt (1977), indicated that juvenile emydid turtles would perform well in a choice situation if rewarded with food. The objective of this experiment was to determine if juvenile turtles could discriminate between two juvenile conspecifics or congeners with the use of a T-maze. T-mazes were used in several studies involving turtle learning abilities (reviewed in Boycott and Guillery, 1962; Burghardt, 1977; Heidt and Burbidge, 1966; Spigel, 1963). Trillmich (1976) successfully used Y-mazes to train and test budgerigars (*Melopsittacus undulatus*) to discriminate between conspecifics. To verify that animals are responding appropriately based on an ability to recognize individuals, it is necessary to rule out obvious differences, such as a large size differential. In this and the following experiment the turtles serving as positive and negative stimuli were chosen from the pool of available animals based on their close physical resemblance.

Materials and Methods

One *Pseudemys floridana* and two *P. nelsoni* juveniles were tested for their ability to discriminate between two *P. floridana* juveniles. All animals were captured in Rock Springs run, Apopka, Florida, in August 1985 and released in June 1986. Juveniles were

used because of the difficulty of maintaining and testing large adults in the laboratory. The measurements of the turtles at the end of the experiment are given in Table 1.

The animals were maintained and tested in their home enclosure, a round, plastic wading pool, 137 cm in diameter, filled to a depth of 23 cm. Several cinder blocks provided hiding places and supported a wooden basking platform. The room was illuminated with standard fluorescent lamps on a 12L:12D cycle. Part of the basking platform was warmed for 8 h/day with a 275 W Sun lamp suspended 30 cm above it. Mean room temperature was 28.5°C ± 1.4°C S.D. The animals were fed to satiation with frozen or live crickets, cat food, and lettuce after training or testing, three times/week. A Plaster-of-Paris block, from which they would break off and ingest small pieces, provided a source of calcium. Turtles would also occasionally ingest each others' feces. Water was filtered through a piece of foam cut to fit around a small submersible pump.

A T-maze, used for training and testing the turtles in these experiments, was constructed from plywood and painted with white marine epoxy (Fig. 1). The ends of the T were fitted with hinged doors that could be opened by pulling on a string. The doors served two functions; they prevented water from flowing through the maze, which might bias an animal's choice, and they prevented other animals from entering the maze. At the choice point, the maze was cut to accept two wire baskets holding the stimuli. The mesh was large enough to permit the subjects to insert their heads into the baskets to nose the stimuli. Turtles used as stimuli were free to turn within the baskets, thus the subjects were usually not presented with two turtles facing the same direction.

Training

For three months prior to testing, one *Pseudemys nelsoni* (subject 2) and one *P. floridana* (subject 1) were trained to orient (turn) toward various cues placed in the wire baskets (Table 2). At first, two colored squares (each 103 cm^2) served as stimuli in the training trials. Successively closer approximations to the test conditions were used in subsequent blocks. A block of trials lasted about one h with three or four blocks conducted in a week; the number of trials in a block depending on how quickly the subjects ran the maze. Baskets containing the stimuli were switched randomly, determined with a coin toss, between the two positions to eliminate turning bias, with the constraint that the stimuli were not in the same position on more than three successive trials (Trillmich, 1976). During a block of trials the stimuli remained in the same basket. Although the baskets appeared virtually indistinguishable, the stimuli were not presented in the same basket for more than three successive blocks.

Trials were conducted after 1600 h to ensure that animals had opportunity to bask earlier in the day. A block of trials commenced when I turned off the heat lamp, placed the maze in the water, where it floated, and the stimuli in the baskets. The baskets were clipped together and placed into the opening at the choice point. Each trial began when I placed the subject in the maze at the starting point, waited until it passed one of the two cages, and then opened both doors. If the subject made the correct choice it was rewarded with one or two crickets which were always eaten. If not, it was returned to the starting point and had to rerun the maze until the correct choice was made. After about three weeks of training, the animals would often swim near the starting point of the maze, as if waiting to be put back in. The relatively low percentage of correct responses in Table 2 suggests that these animals had difficulty learning this paradigm (see Shettleworth, 1984).

Testing

For the duration of the testing period, two juvenile *Pseudemys floridana*, matched for size and pattern, were used as the stimuli to discriminate. If the subject turned down the arm of the maze containing the "+" individual, a correct choice was scored. The test procedure differed from the training procedure because the animals were allowed to leave the maze whether or not they turned in the correct direction, but were only rewarded if the correct choice had been made. Additionally, a second untrained *P. nelsoni* (subject 3) was included during testing since it accepted food immediately after being placed in the maze.

The significance of the percent correct for all trials was tested using the normal approximation to the binomial (one-tailed, Hines and Montgomery, 1980).

Results

In this series of tests, one of the turtles performed significantly better than chance and two did not (Fig. 2). The subject that performed the best was the juvenile *P. floridana* (67.6%), as might be expected because it was discriminating between two conspecifics. Neither the untrained *P. nelsoni* (subject 3, 56.4%) nor the trained *P. nelsoni* (subject 2, 51.0%) performed well. Subject 2 also performed less well than the *P. floridana* juvenile during training sessions (Table 2) and was prone to panic, although it would accept food if it made the correct choice.

CHAPTER 3

EXPERIMENT 2

Introduction

Since results from the first experiment demonstrated that at least one individual could discriminate between two similar conspecifics when positively reinforced, a second experiment was initiated. The objective was to replicate the positive findings of the first experiment using additional subjects and a modified methodology. It was hoped that the lengthy training period using stimuli other than turtles could be eliminated by punishing incorrect choices. The learning literature suggests that the most efficient way to suppress a response is to punish it if a nonpunished alternative is available (Fantino, 1973). The subjects were not rewarded, allowing more trials to be administered in the same amount of time.

Materials and Methods

Subjects consisted of five newly caught juvenile *Pseudemys nelsoni* and one juvenile *P. floridana* from Alachua County, Florida. Their measurements are given in Table 3. Two of the *P. nelsoni* served as stimuli. They were not as closely matched for size as were the two *P. floridana* in the previous experiment. The subjects were not trained or rewarded for correct responses. During testing they were allowed to exit the T-maze if they turned in the correct direction, otherwise they were forced to rerun the maze. If they did not turn correctly on their third attempt they were placed in a bucket until their next trial as

punishment. This procedure was run for 16 weeks. The number of trials/block was greater later in the experiment as the turtles negotiated the maze more quickly and with fewer errors.

I tested the significance of the percent correct using the normal approximation to the binomial (one-tailed, Hines and Montgomery, 1980).

Results

This procedure did not work as well as the procedure used in experiment 1, as subjects often panicked when put in the maze, even after many weeks of testing and took much longer to perform well. I divided the trials into two approximately equal groups and tested each separately for significance (Fig. 3). Further subdivisions were not made because additional information gleaned from the data was offset by a loss of statistical power. In the first group, only the *Pseudemys floridana* juvenile did better than chance at discriminating between the two *P. nelsoni* in the baskets. All animals except subject A appeared to be making the discrimination by the end of the experiment but none did as well as subject 1 in the previous experiment. Even subject A improved towards the end of the experiment. In the last 8 blocks (146 trials) this subject averaged 61% correct ($p = 0.004$, binomial test).

CHAPTER 5

DISCUSSION

The results suggest that juveniles of both species may be able to discriminate between two similar conspecifics in the laboratory and that juvenile *Pseudemys floridana* can discriminate between two similar *P. nelsoni*. Although these experiments do not prove that these turtles have individual recognition, they do suggest that the animals possess the sensory and memory capabilities necessary for its existence.

Olfaction is probably the sensory modality used by turtles, at least initially, to recognize others. Individual recognition is mediated by odors in many animals (reviewed in Halpin, 1980). Turtles often nosed the stimuli during training and testing during this study, and each other during social interactions in nature (Kramer, 1986).

Given the length of the training period, number of trials in both experiments, and disposition of the animals during testing, I suggest that the method of positively reinforcing correct choices (Experiment 1) yields better results with turtles than negatively reinforcing them for incorrect choices (Experiment 2). Subjects in the first experiment panicked infrequently and appeared eager to enter the maze. In contrast, subjects in the second experiment hid under the maze or in the cinder block cavities while other subjects were tested.

The results of the two experiments are not, however, directly comparable. Trained animals in Experiment 1 probably did not find the testing apparatus aversive, while those in Experiment 2 probably did, in addition to their incorrect choices being punished. Mrosovsky (1964), in a paradigm conceptually similar to Experiment 2, obtained clearer results on a simpler task using *Trachemys scripta*. His subjects were placed on a dry

platform in front of the experimenter (presumably an aversive condition) and given a choice of plunging into a white or black, water filled compartment. Once a preference had been established, the subjects were shocked (punished) for making their preferred choice to effect a choice reversal. After an average of 733 trials most of the turtles had either reduced the percentage of time they chose their preferred "color" (brightness) or would not dive in.

It is often frustrating to try to empirically demonstrate mental abilities that animals appear to use in the field (Cheney et al., 1986). Although data to examine the following point were not taken, the major difficulty in Experiment 1 appeared to be the subjects' inability to consistently pass the basket holding the positive stimulus, rather than stop in front of it, in order to be rewarded when exiting on that side. In many trials the subjects would initially turn correctly, but then stop in front of the basket, sometimes for a minute or more. In some of these cases they did not continue in the same direction and so were not rewarded. Their poor performance is evident when the percent correct of the training and testing blocks (Table 2 and Fig. 2) are compared. In few blocks of trials were animals earning rewards more than 80% of the time. Similar difficulties have been reported by Butler and Johnson (1972) who tested operantly trained sunfish (*Lepomis macrochirus*) for individual discrimination. They found that their subjects did not meet their (unstated) criterion, although they apparently performed better than chance (p not given). Petrillo and Powers (1987) had to use very modest criteria for testing spatial learning in the turtle, *Chrysemys picta*.

A further drawback to using trained animals is that subjects may attend to details irrelevant to the animals in nature. An advantage of using trained animals is that one may easily manipulate aspects of the stimuli and sensory avenues to determine which are important, as in Trillmich's (1976) budgerigar study. This advantage was not exploited here.

Punishing turtles (Experiment 2) adversely affected the performance of these animals to the point where hundreds of trials were needed to show signs of improvement (Fig. 3). This or a similar procedure is not recommended for testing discriminative abilities of turtles.

In some studies, individual discrimination has been inferred by noting behavioral responses to the presentation of various cues or by observing changes in repeated interactions. Examples of these are Zayan's (1974, 1975) studies of the fish, *Xiphophorus*, work on various catfish and cichlids (reviewed in Colgan, 1983; Zayan, 1974), discrimination of cloacal odors in the salamander, *Plethodon cinereus*, (Simon and Madison, 1984) and neighbor recognition, in *Plethodon cinereus* (Jaeger, 1981) and the lizard, *Dipsosaurus* (Glinski and Krekorian, 1985). Manipulation of social contexts to infer individual discrimination, rather than training subjects to demonstrate individual recognition capabilities, may be better suited to these taxa. Reliance is not placed on learning abilities but on observable, natural patterns of behavior. In light of the difficulties encountered during the present study, this approach should be considered in future research on this topic using turtles.

LITERATURE CITED

Andrews, R.M. 1985. Mate choice by females of the lizard, *Anolis carolinensis*. J. Herpetol. 19, 284-289.

Auth, D.L. 1975. Behavioral ecology of basking in the yellow- bellied turtle, *Chrysemys scripta scripta* (Schoepff). Bull. Florida State Mus. Biol. Sci. 20, 1-45.

Boycott, B.B. and R.W. Guillery. 1962. Olfactory and visual learning in the red-eared terrapin, *Pseudemys scripta elegans* (Wied). J. Exp. Biol. 39, 567-577.

Burghardt, G.M. 1977. Learning processes in reptiles. *In* Gans, C. and D. Tinkle (Eds.). The Biology of the Reptilia, vol. 7. Academic Press, N.Y. Pp. 555-681.

Bury, R.B.J., J.H. Wolfheim, and R.A. Luckenbach. 1979. Agonistic behavior in free-living painted turtles (*Chrysemys picta bellii*). Biol. Behav. 179, 227-239.

Butler, M. and D.A. Johnson. 1972. A test of individual recognition in bluegill sunfish using operant procedures. Virg. J. Sci. 23, 149.

Casteel, D.B. 1911. The discriminative ability of the painted turtle. J. Animal Behav. 1, 1-28.

Cheney, D.R., R. Seyfarth, and B. Smuts. 1986. Social relationships and social cognition in nonhuman primates. Science 234, 1361-1366.

Colgan, P. 1983. Comparative Social Recognition. John Wiley & Sons, N.Y. 281 pp.

Crews, D. 1985. Inter- and intraindividual variation in display patterns in the lizard, *Anolis carolinensis*. Herpetologica 31, 37-47.

Dugan, B. 1982. A field study of the headbob displays of male green iguanas (*Iguana iguana*): Variation in form and context. Anim. Behav. 30, 327-338.

Evans, L.T. 1940. Effects of testosterone propionate upon social dominance in young turtles, *Chrysemys picta*. Biol. Bull. 79, 371.

Evans, L.T. 1952. Endocrine relationships in turtles. III. Some effects of male hormone in turtles. Herpetologica 8, 11-14.

Evans, L.T., W. Preston, and E. Hardy. 1973. Imprinting in *Chrysemys* turtles. Am. Zool. 13, 1269 (abstr. 4).

Evans, L.T., W. Preston, and M.E. McGeary. 1974. Imprinting in turtles. Am. Zool. 14, 1278 (abstr. 352).

Fantino, E. 1973. Aversive control. *In* Nevin, J.A. and G.S. Reynolds (Eds.). The Study of Behavior: Learning, Motivation, Emotion, and Instinct. Scott, Foresman and Co. Glenview, Ill. Pp. 238-279.

Ferguson, G.W. 1971. Observations on the behavior and interactions of two sympatric *Sceloporus* in Utah. Amer. Midl. Nat. 86, 190-196.

Glinski, T.H. and C. O'Neil Krekorian. 1985. Individual recognition in free-living adult male desert iguanas, *Dipsosaurus dorsalis*. J. Herpetol. 19, 541-544.

Halpin, Z.T. 1980. Individual odors and individual recognition: Review and commentary. Biol. Behav. 5, 233- 248.

Harless, M. 1979. Social behavior. *In* Harless, M. and H. Morlock (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, N.Y. Pp. 475-492.

Heidt, G.A. and R.C. Burbidge. 1966. Some aspects of color preference, substrate preference and learning in hatchling *Chrysemys picta*. Herpetologica 22, 288-292.

Hines, W.W. and D.C. Montgomery. 1980. Probability and Statistics in Engineering and Management Science, 2nd ed. John Wiley & Sons, N.Y.

Jaeger, R.J. 1981. Dear enemy recognition and the costs of aggression between salamanders. Am. Nat. 117, 962-974.

Johnson, V.R. 1977. Individual recognition in the banded shrimp *Stenopus hispidus* (Oliver). Ani. Behav. 25, 418-428.

Kramer, M. 1986. Field studies on a freshwater Florida turtle, *Pseudemys nelsoni*. *In* Drickamer, L.C. (Ed.). Behavioral ecology and population biology. Privat, I.E.C. Toulouse, France. Pp. 29-34.

Lardie, R.L. 1983. Aggressive interactions among melanistic males of the red-eared slider, *Pseudemys scripta elegans* (Wied). Bull. Oklahoma Herpetol. Soc. 8(4), 105-117.

Lovich, J.E. 1984. An analysis of aggressive basking behavior in the eastern painted turtle. Master's Thesis, George Mason University. 79 pp.

McBride, G. 1964. A general theory of social organization and behaviour. Univ. of Queensland Fac. Papers Vet. Sci. 1(2), 75-110.

McDonald, D.M. 1987. The significance of male dewlap color in female mate selection of *Anolis carolinensis* (Iguanidae) from south Florida. Master's Thesis, University of Tennessee, Knoxville. 55 pp.

McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc, Zool. Soc. London 143, 239-279.

Mrosovsky, N. 1964. Modification of the diving-in response of the red-eared terrapin, *Pseudemys ornata callirostris*. Quart. J. Exp. Psychol. 16, 166-171.

Petrillo, M.A. and A.S. Powers. 1987. Disruption in maze performance after cortical lesions in turtles (*Chrysemys picta*). Soc. Neurosci. Abs. 13, 1125.

Simon, G.S. and D.M. Madison. 1984. Individual recognition in salamanders: Cloacal odours. Anim. Behav. 32, 1017-1020.

Shettleworth, S. 1984. Learning and behavioural ecology. *In* Krebs, J.R. and N.B. Davies (Eds.). Behavioural ecology: An evolutionary approach, 2nd ed. Sinauer Assoc., Inc., Sunderland, Mass. Pp. 170-194.

Spigel, I.M. 1963. Running speed and intermediate brightness discrimination in the freshwater turtle, *Chrysemys*. J. Comp. Physiol. Psych. 56, 924-928.

Trillmich, F. 1976. Spatial proximity and mate-specific behaviour in a flock of budgerigars (*Melopsittacus undulatus*). Z. Tierpsychol. 41, 307-331.

Zayan, R.C. 1974. Le rôle de reconnaissance individuelle dans la stabilité des relations hierarchiques chez *Xiphophorus* (Pices, Poeciliidae). Behaviour 49, 268-312.

Zayan, R.C. 1975. Défense du territoire et reconnaissance individuelle chez *Xiphophorus* (Pices, Poeciliidae). Behaviour 52, 266-312.

APPENDIX

TABLES AND FIGURES

Table 1. Measurements of turtles, *Pseudemys nelsoni* and *P. floridana*, used in Experiment 1.

Species	Plastron Length (mm)	Carapace Length (mm)	Carapace Width (mm)	Mass (g)
1. *Pseudemys floridana*	128	139	111	416
2. *Pseudemys nelsoni*	119	126	102	347
3. *Pseudemys nelsoni*	83	86	72	125
+ *Pseudemys floridana*	103	114	93	250
- *Pseudemys floridana*	110	121	95	269

Note: Numbers preceding subjects refer to subject ID. Symbols refer to turtles used as "+" or "-" stimuli.

Table 2. Stimuli and results of training sessions, in order, in Experiment 1.

Stimulus		No. Blocks	No. Trials		% Correct		p (Binomial test)	
			Subject		Subject		Subject	
Positive	Negative		1	2	1	2	1	2
green square	red square	4	42	48	85.7	68.8	<0.01	<0.01
green square + juv. *P. nelsoni*	red square	4	42	43	71.4	58.1	<.01	0.18
juv. *P. nelsoni*	red square	2	23	17	43.5	52.9	0.80	0.50
juv. *P. nelsoni*	empty	3	28	27	57.0	44.4	0.29	0.78
juv. *P. nelsoni*	juv. *P. floridana*	13	209	210	66.5	56.7	<0.01†	0.03†

Note: Subject 1 was a *P. floridana* and subject 2 a *P. nelsoni*.

†normal approximation to the binomial.

Table 3. Measurements of turtles used in Experiment 2.

Species	Plastron Length (mm)	Carapace Length (mm)	Carapace Width (mm)	Mass (g)
A. *Pseudemys nelsoni*	116	127	103	334
D. *Pseudemys nelsoni*	74	78	66	82
E. *Pseudemys nelsoni*	71	76	69	87
F. *Pseudemys floridana*	69	76	68	74
+ *Pseudemys nelsoni*	105	112	94	240
- *Pseudemys nelsoni*	111	122	93	297

Note: Letters preceding subjects refer to subject ID. Symbols refer to turtles used as "+" or "-" stimuli.

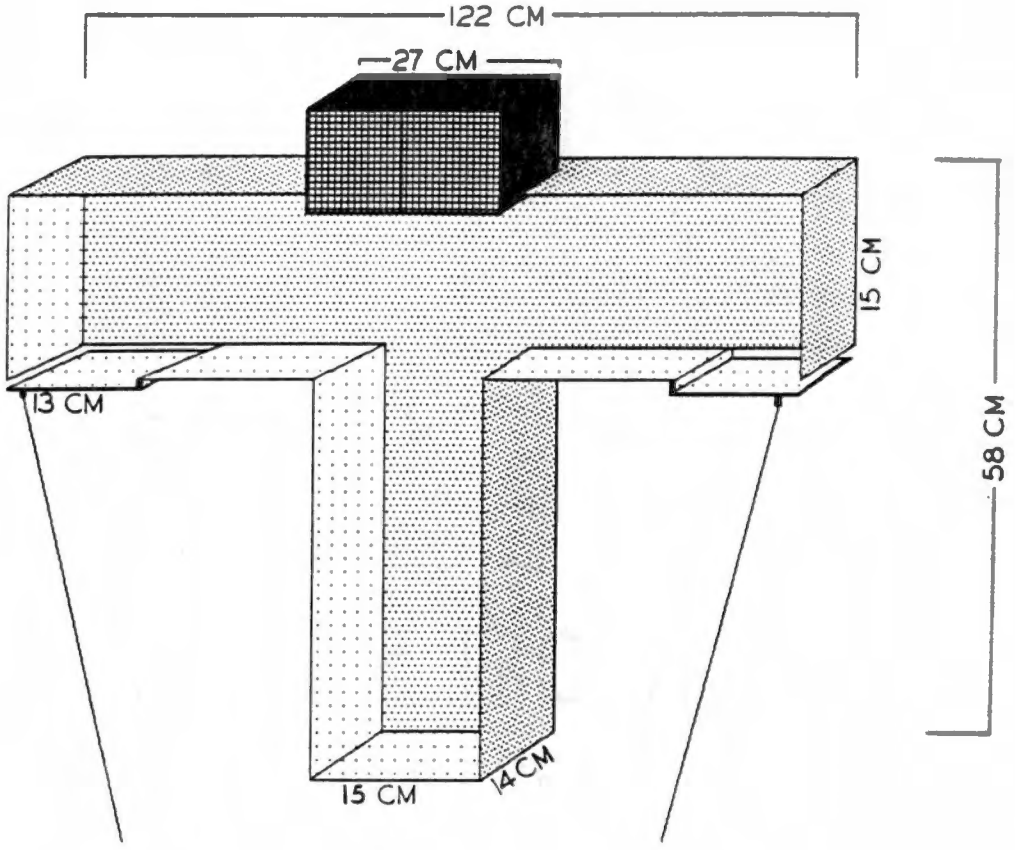

Figure 1. T-maze used in Experiments 1 and 2. The T-maze (not to scale) floated but was about two-thirds full of water during training and testing of *Pseudemys nelsoni* and *P. floridana*. Subjects were placed at the bottom of the "T".

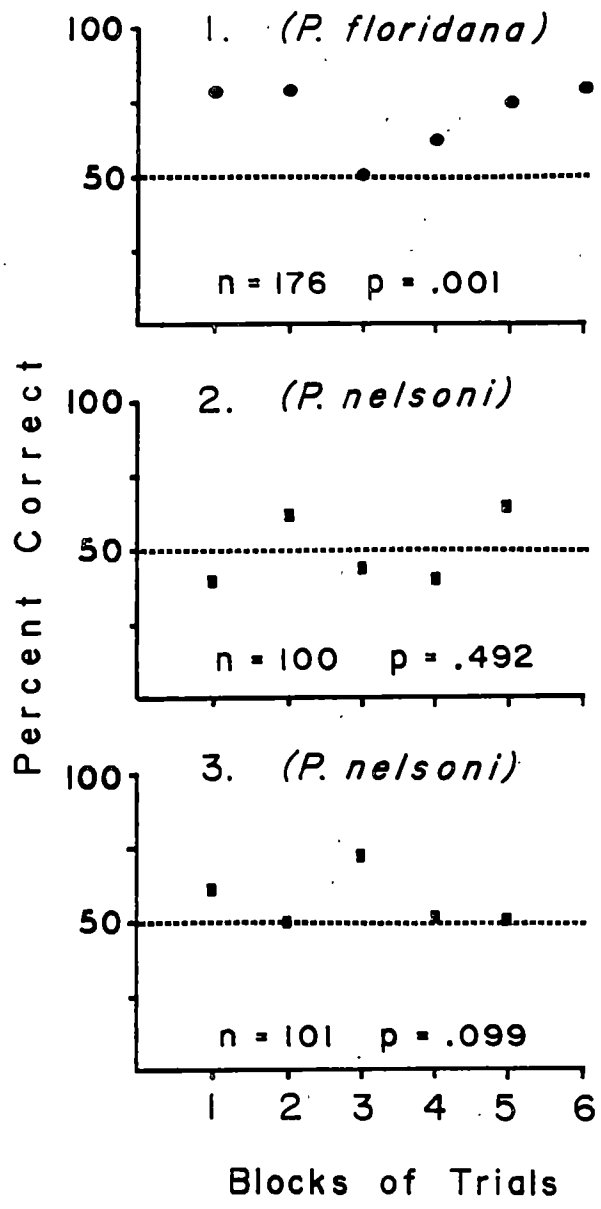

Figure 2. Percent correct of each block of trials for subjects in Experiment 1 (*Pseudemys nelsoni* and *P. floridana*). Subject 1 (*Pseudemys floridana*) received substantially more trials than the other two (*Pseudemys nelsoni*). Subject 3 was untrained.

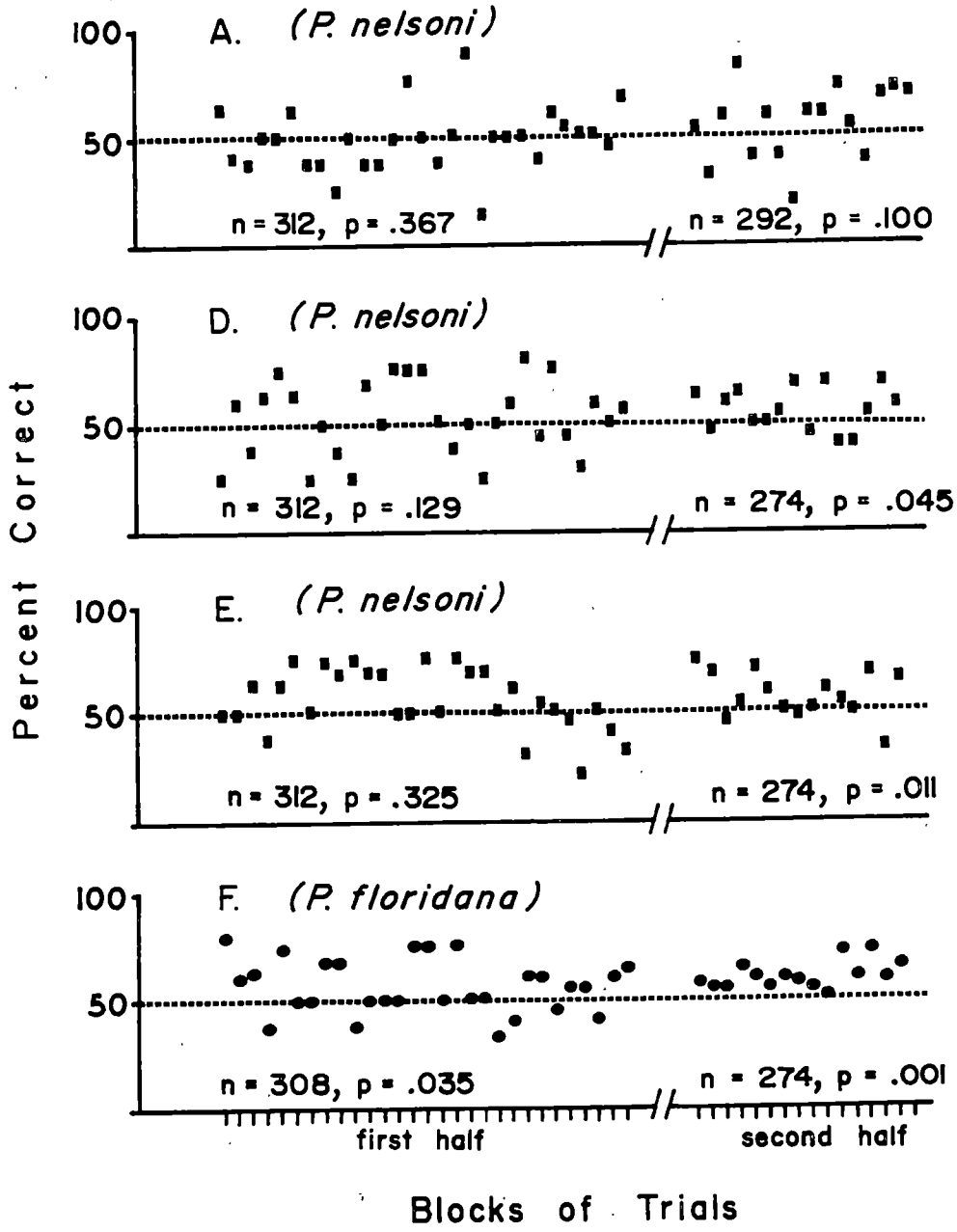

Figure 3. Percent correct of each block of trials for subjects (*Pseudemys nelsoni* and *P. floridana*) in Experiment 2. The blocks were divided into two groups and the significance of each group for each turtle was tested separately.

PART 7

THE HOME RANGE OF *PSEUDEMYS NELSONI*

CHAPTER 1

INTRODUCTION

Home range, the relatively small area some animals restrict their movements to, has become a standard ecological parameter. Home range size is often correlated with body size, ecology and behavior (Damuth, 1981; Polis, et al., 1985), and can be useful in inter- and intra-specific comparisons. Measures of home range are largely concerned with approximating the boundaries of an area within which an individual is likely to be found. However, it is also important to assess usage of the bounded area, that is, which parts of a home range are visited most frequently and which parts rarely (Jorgensen and Tanner, 1963). Uneven usage may reflect a heterogeneous resource distribution within the home range. In studies concerned with an animal's social system, home range usage may provide clues to the number of other individuals typically encountered (Jorgensen, 1968).

There are several methods for modelling home ranges from which size may be calculated. These include circles, ellipses, and various types of polygons (Anderson, 1982). Unfortunately, dissimilar methods may give different results, making comparisons of results and conclusions difficult or impossible. Home range usage (utilization distributions) can be calculated for an individual if sufficient relocations exist or, if the number of relocations/individual is small, averaging over many individuals using mathematical techniques (Ford and Krumme, 1979).

Home range size of semi-aquatic turtles is usually estimated using the minimum convex polygon technique (Southwood, 1966) or Sexton's (1959: 137-138) definition, the "minimum direct distance over water between the two most distant points of capture". The latter is especially useful for turtles inhabiting rivers or streams. Some species have

extensive home ranges, e.g., *Trionyx* (Plummer and Shirer, 1975), whereas others have relatively small home ranges, e.g., *Sternotherus* (Mahmoud, 1969).

The focus of this Part is to describe the size and usage of the home range of *Pseudemys nelsoni* (Emydidae). Ascertaining how individual *Pseudemys nelsoni* use their home range was in part prompted by asking if movements of individuals were consistent with a social system based on individual recognition, given field observations (see Part 2) and the ability of these turtles to be trained to discriminate among individuals (see Part 6). Data collected on *P. floridana* inhabiting the study site are included for comparative purposes.

CHAPTER 2

MATERIAL AND METHODS

The main study site comprised a 980 m section of Rock Springs run, located 2 km downstream from Rock Springs, Apopka, Orange Co., Fla. Adult pseudemid turtles of both species were captured indiscriminately and, after marking, released near the point of capture. A number was painted on the carapace in four places with a rubberized paint marker (Sport Divers Mfg. felt tip marker) or epoxy paint. The painted number was discernable for one to three months. Animals were also marked permanently by drilling one to three small holes in the first three or last five marginals (Cagle, 1939) through which a small plastic tag was inserted. The tags remained in place for about one year. The tags proved useful in identifying marked animals because the holes often became obscured by algae. More time was spent collecting turtles in areas where they could be easily located, thus capture effort was not equal throughout the study site.

Obtaining good estimates of both population density and home range size requires different data collection techniques. To calculate population density, a large number of individuals must be marked, whereas to gather data on animal movements requires careful monitoring of selected individuals; both techniques are time intensive. Since the major thrust of the project was behavioral, a compromise was effected by marking animals exclusively in the first few days of each study period and relocating animals during censusing of basking animals, behavioral observations, from a canoe or other fortuitous circumstances, and weekly searches throughout the study area and adjacent portions of the run. Relocations were made intermittently over a three year period (1983 - 1985). Basking

animals were censused to estimate population size using the Bailey triple catch method (Begon, 1979, see Part 2).

Three animals were radio tagged at Payne's Prairie, Gainesville, Alachua Co., Fla., and relocated at least daily for 24 days. The habitat of Payne's Prairie differs considerably from Rock Springs run (see Part 2). Radio tracked animals remained in a shallow lake, created by a dam, until the water level fell. Two then moved to a canal bordering the lake.

The plastron length of captured males at Rock Springs run measured 224 mm ± 25 S.D., females 267 mm ± 32 S.D. The radio tracked male at Payne's Prairie measured 231 mm, the two females 306 mm and 295 mm.

Analysis of Relocations at Rock Springs Run

Two methods were used to calculate home range size. In one, I used the maximum distance over water between relocations (Sexton, 1959) to compute linear home range size. In the second, I adapted Ford and Krumme's (1979) procedure, to construct a best-fit "composite" home range (population utilization distribution) for different classes of animals. In addition, the latter technique estimates home range usage.

Linear home range size

All relocations of each turtle were plotted on scale maps of the study site. The two most distant relocations were used to estimate the home range perimeter. Individual turtles were often seen crossing the river, thus I assumed that individuals used the full width of the river. The resulting distances were regressed on plastron length, time between

relocations, and the number of relocations per individual. Sex differences were tested using the Mann-Whitney U-test.

Population utilization distribution

The distances between all pairs of relocations of each animal in a certain class (e.g., male *Pseudemys nelsoni*) were classified into discrete categories (the relocation distance function). I used the following categories: within 10 m, 10-20 m apart, 20-30 m apart, etc., to 990-1000 m apart (Fig. 1). GRG2, a FORTRAN program for solving constrained nonlinear optimization problems, was then used to reconstruct composite home ranges. In essence, the program returned the proportion of relocations coming from each of the 100 "grids" of the composite home range, based on the relocation distance function. The program simultaneously minimized the squares of the differences between the values of the relocation distance function determined from the data and those generated by the solution. It was constrained because the proportions (from each of the 100 "grids") of the solution must sum to one. The program was usually unable to find a solution that exactly satisfied the imposed conditions, but the relocation distance function from the solution had approximately the same distribution as the relocation distance function from the solution. The greatest difference was that the program was often unable to fit the tail end of the relocation distance function (the few relocations separated by large distances) into the solution. Unlike variation attributed to the optimizer for solutions in two dimensions, reported by Ford and Krumme (1979), solutions for my (linear) data were identical if the same starting point and initial proportions (used to "center" the solution in the grids) were entered into the program. Solutions from other sets of initial proportions differed so little or not at all that several runs using the same data were unnecessary.

One of the assumptions for using all relocations is that the relocations are time independent. Figure 2 indicates that the distance moved between locations was not a function of the time between them. Similar results have been shown for small mammals using another statistical technique (e.g., Swihart and Slade, 1985). An additional assumption is that a composite or "average" home range can be interpreted. If sufficient relocations were available for each individual, the distribution of probabilities of recaptures throughout the home ranges should resemble each other and a solution based on many individuals but with few relocations per individual. Only on one turtle at Rock Springs run, a male *Pseudemys nelsoni*, were sufficient relocations made to use Ford and Krumme's (1979) technique. The utilization distribution for this animal, based on 55 pairs of relocation distances, was similar to population utilization distributions composed of 42 - 45 pairs of relocation distances drawn randomly from other males.

When comparing classes of animals, a problem emerges: since solutions are not unique, they cannot be directly compared. It is possible that several solutions fit the data about equally well, the solution given by a program reflecting both variations among programs for solving these problems, degree of resolution used or accuracy sought when searching for a solution (these are often user defined), randomness that the optimizer may induce, the starting values for the optimizer, and the occasional sensitivity of the solution to small changes among proportions of relocation distances. Ford and Krumme (1979) suggest a reliable and easily interpretable alternative. By plotting the minimum distance that will contain a certain percent of the relocations (cumulative probability of recapture), one can compare two or more solutions by the shape of the curves. Further, a group can be subdivided and the solutions of each plotted to examine the variance of the solutions. One can thus obtain a mean minimum distance and its variance at any probability.

The cumulative probabilities of recapture and minimum distances containing these probabilities were calculated following Ford and Krumme (1979). Corridors, regions within the composite home range where the probability of recapture is zero, are not included in minimum distances. The probability of recapture at each 10 m grid of the home range was plotted on graph paper, the probabilities then connected with straight lines. At each change in slope or with the addition of a new peak, a distance for that level was calculated by summing the distance below each of the peaks at that level (Fig. 3). In addition, the area under the curve at each level was calculated with simple trigonometry. The total area under the curve was then divided into each of the successive cumulative areas to give a probability corresponding to the distance at that level.

This technique was applied to the following data sets: all male *Pseudemys nelsoni*, with and without basking relocations, all female *P. nelsoni*, with and without basking relocations, all female *P. nelsoni* excluding relocations during the nesting season, four subgroups of male and three of female *P. nelsoni*, male and female *P. nelsoni* combined, and male and female *P. floridana* combined. There were insufficient relocations for *P. floridana* to further subdivide this group. Sample sizes for each data set are given in Table 1.

Basking site locations in the home range

A comparison of population utilization distributions from data sets with and without basking relocations suggested that most home ranges were established with a basking site at the up- or downstream edge. To test this statistically one must calculate expected frequencies for the sample based on the likelihood of basking relocations occurring at the edge of the home range by chance. For example, if an individual was relocated five times,

once while basking, the probability that the basking relocation is one of the two edge relocations is 2/5. If two relocations were located near each other (< 10 m) at one edge, so that of five relocations, three were near one of the two edges, the probability that the basking relocation was one of the three is 3/5. To calculate the expected frequency of basking relocations at home range edges for the sample, the probabilities of edge relocations of individual turtles were summed. The expected frequency of basking relocations for the sample in positions other than the up- or downstream edge was calculated as the sample size (32) minus the expected frequency of basking relocations at home range edges. Using a G-test for goodness of fit, the expected frequencies were compared with observed frequencies, the number of individuals in the sample divided into those with basking relocations at the home range edge and those without basking relocations at the home range edge.

The sample used for this test included only individuals for which expected probabilities could be determined, i.e., with at least three locations including a basking relocation. Some individuals were repeatedly observed basking on the same basking site. For the calculations described above, I included a basking site only once when counting basking relocations. If more than one basking relocation at different basking sites were made, expected probabilities were calculated as the number of possible combinations with at least one basking relocation at an edge divided by the number of relocations taken Y (where Y = the number of basking relocations) at a time. For example, if six relocations, two of the animal basking at different sites were made, the expected probability of at least one basking relocation located at an edge by chance is 3/5.

Telemetry

Three *Pseudemys nelsoni* in Payne's Prairie were outfitted with a radio transmitter of approximately 27 mHz, wired to two holes drilled through the rear marginals of the carapace. Relocations were taken at least daily for 24 days, from 27 June 1986 to 20 July 1986. Movements of these animals were plotted on scale maps of the area.

CHAPTER 3

RESULTS

Linear Home Range Estimates

Estimates of home range size for *Pseudemys nelsoni* were very variable, ranging from 0 to 972 m (Table 2). These estimates were not a function of the number of relocations per individual (Fig. 4a, b; $p > 0.25$) nor the number of days between relocations (Fig. 4c, d; $p > 0.25$). Similarly, there were no sex differences or effects of body size ($p > 0.25$). Most relocated animals moved little among relocations (Fig. 1). Even after several years I found few marked turtles outside the study site.

While no relocated *Pseudemys floridana* had moved more than 684 m, mean home range estimates were larger. In addition, both the mean number of relocations per individual was smaller and a smaller percent of marked animals were relocated (Table 2).

Population Utilization Distributions

All relocations of male and female *Pseudemys nelsoni*, including basking site relocations, were used to construct a population utilization distribution for each sex. Both distributions exhibit a very large peak near one end of the home range (Fig. 5a, b). This may be because individuals were frequently relocated at the same basking site, giving rise to a large proportion of relocations within 10 m of a previous one. If the large peak was due to basking relocations, the results suggest that basking sites are usually located at one end of a home range rather than in the middle. This hypothesis was tested using a G-test

for goodness-of-fit (Table 3). No statistical difference was found between the observed and expected frequencies. Thus, basking relocations are not more likely to be found at the up- or downstream edge of the home range. However, the large peak in each of the composite home ranges is probably due to basking relocations since, after removing the basking relocations from the data (Fig. 6a, b; based exclusively on recaptures and resightings of animals in the water), the resulting population utilization distributions lost this single large peak. As most social interactions occur in the water, the data were reanalyzed without basking site relocations to estimate size and usage of the aquatic portion of the home range.

Population utilization distributions for males or females (Fig. 6a, b) are smaller than the mean home range size estimated using Sexton's (1959) definition, consistent with Anderson's (1982) finding that Ford and Krumme's (1979) technique underestimates home range by about 25%. Since female *Pseudemys nelsoni* may leave their regular home ranges during the nesting season, I removed summer relocations (Jackson, 1988) of females and recalculated their population utilization distribution (not illustrated). The resulting home range estimate was actually slightly larger than the estimate with summer relocations. Thus, I concluded that nesting movements were not affecting the home range size estimates. To test for sex differences, males and females were first subdivided into groups with 39 - 55 pairs of relocation distances/group. A composite home range was then constructed for each of these data sets and results graphed as probability vs. minimum distance (Fig. 7). There were no significant differences between males and females, whether using 0.95 or 0.50 probability (the latter suggested by Anderson, 1982). Data of both sexes were therefore combined and a population utilization distribution and probability vs. minimum distance for all *Pseudemys nelsoni* calculated (Fig. 8a, b). Since data for *Pseudemys floridana* were insufficient for subgrouping, calculations were made for both

sexes combined (Fig. 9a, b). It is clear that by using either a linear measure or Krumme and Ford's technique, the home range of *P. nelsoni* is smaller than that of *P. floridana*. This is consistent with a higher relocation rate for *P. nelsoni* since *P. floridana* individuals, with a larger home range, would be more likely to include areas outside the study site.

Using Ford and Krumme's (1979) technique, the average home range for *Pseudemys nelsoni* appears to comprise about 120 m of river length including a short "corridor" in which the animal is unlikely to be relocated. In comparison, the average home range of *P. floridana* is about 650 m with many corridors of various lengths.

Microhabitat Preferences

The population utilization distribution for *Pseudemys nelsoni* suggests that individuals do not use their home range evenly, possibly resulting from a heterogeneous resource distribution. I speculate that the patchy distribution of resting sites is the most likely heterogeneously distributed resource to explain the distribution of relocations. While microhabitat variables were not quantified in this study, I offer the following generalizations, based on a subjective evaluation of microhabitat in the study site. Turtles were most often captured and relocated in or near areas that provided support for animals resting near the surface, either emergent vegetation (e.g., *Nuphar* sp., *Pontederia* sp., or *Typha* sp.) or submerged trees, branches or piles of branches derived from shoreline vegetation (Fig. 10). Animals appeared to prefer resting sites with overhanging vegetation. They were rarely found in shallow water adjacent to the bank. There were few relocations from animals in the middle of the run, places with strong currents, or where water was deeper than about two m, although turtles were seen in all these situations on occasion.

The distribution of basking sites was also important since areas without them rarely yielded turtles.

Telemetry

Movements of radio tracked animals were apparently erratic. Animals appeared to spend a few days in a small area, then move to another area and stay there for a few days. On July 13, the male burrowed into the mud, probably for aestivation, and remained there until he was dug up to remove the transmitter on July 16. Due to a drought, lake levels were falling rapidly at this time and two days later both females moved into a canal bordering the lake and a dike. I terminated data collection on July 20 because the turtles were excluded from moving freely about the study area, due to both the drought and potential predation from the numerous large alligators that congregated in regions of the lake still holding water. These results (Fig. 11) also indicate that movements tend to be limited to a relatively small area.

Frequency of Encounters

The population density of adult pseudemid turtles in the Rock Springs run study site was 250 ± 75 S.D. Using the proportion of *Pseudemys nelsoni* to *P. floridana* captured to estimate the proportion in the study site, about 188 (75%) were *P. nelsoni* and 62 (25%) were *P. floridana.* If one assumes that home ranges were distributed evenly in the study site, home ranges of *P. nelsoni* should be centered about 5 m apart. Using the above results, which suggest that the home range of *P. nelsoni* is minimally 120 m in length, an individual's home range should partially overlap with the home ranges of at least 50 adult

conspecifics. Of these 50 adult conspecifics, there should be extensive home range overlap (> 50%) with about 25. Thus, the average adult should regularly encounter at least 25 other adult conspecifics at the Rock Springs study site in the course of its daily activities.

CHAPTER 4

DISCUSSION

Results from constructing population utilization distributions of male and female *Pseudemys nelsoni* suggested that individuals typically bask near one end of their home range. If true, basking sites may be a limiting resource, forcing at least some animals to travel to the periphery of their home range to bask, or basking sites may not be located near other resources. However, a reevaluation of the data was not consistent with the hypothesis that basking relocations come primarily from the up- or downstream edge of the home range. This example suggests that results from modeling home ranges using the mathematical technique suggested by Ford and Krumme (1979) must be viewed with caution, and, if possible, validated with other procedures.

An interesting result from this study is the apparent lack of association between time and distance between relocations. One might suspect that, in general, distance between relocations should increase with time, the association weakening until, given enough time, relocations become independent of each other. There are two reasons this relationship may not have been detected in this study. First, the small home ranges of *Pseudemys nelsoni* at Rock Springs run could be traversed by an individual in under an hour. Since very few relocations were made less than one day apart, the time to independence between relocations may have been surpassed by even the closest pair of relocations in time. Second, the effect of diurnal cycles can complicate the relationship between time and the distance between relocations (Swihart and Slade, 1985) such that independence occurs only in a "window" of the 24 h cycle. Individuals may show spatial and temporal fidelity to

certain areas within their home range. Relocations 24 h apart would probably not be independent in this case.

Too few relocations of individuals in the water were made at the Rock Springs run study site to examine this statistically. However, the radiotracked turtles at Payne's Prairie were usually relocated once in the morning and again in the afternoon. If these animals followed a diurnal pattern of movement, there should be some evidence that animals were moving between two areas on a daily basis. The map of these animal's movements (Fig. 11) does not support this conclusion. In contrast, animal's at Rock Springs run usually basked on the same log or group of logs, although probably not daily. Since most basking sites were in full sun only part of the day, basking relocations of individual animals should be fairly predictable. Auth (1975) provides evidence for this in a related turtle, *Trachemys scripta*. Reasons similar to those given above, along with interindividual differences, may also apply to the lack of predictive value of time and number of relocations on linear home range estimates (see below).

Home range research done by others on related species have yielded widely disparate estimates that do not appear to be the result of different methodologies. For example, Pearse (1923) found that most of the painted turtles (*Chrysemys picta*) he marked moved less than 100 m during the course of his study whereas those studied by MacCulloch and Secoy (1983) moved an average of over 2 km, and a single male traveled 6.5 km in one day. The ability of these turtles to travel distances exceeding their home range was noted earlier by Marchand (1945), who stated that his estimated home range of less than 300 yds (277 m) for *Pseudemys floridana* could be covered in a single day. His estimate is less than the 650 m of this study using Ford and Krumme's (1979) technique, but close to the mean using Sexton's (1959) "maximum distance over water" method. Estimates of the

home range and movements of *Trachemys scripta* also differ considerably among studies (reviewed in Bury, 1979, see also Florence and Murphy, 1976; Morreale, et al., 1984).

The great variation among linear home range estimates at the Rock Springs run study site suggests that either 1) there is considerable individual variation in home range size, 2) some individuals maintain home ranges while others are "floaters", 3) some individuals change home range more frequently than others, or 4) individuals have large home ranges but spend most of their time in a core area (Samuel et al., 1985), making the observed variation a problem of sampling. I cannot discriminate among alternatives (1), (2), and (4); however, alternative (3) is unlikely since there is no trend in these data of increasing home range estimates with increasing time between relocations. If (3) were true, larger home range estimates, at least of some individuals, would be expected with increased time among relocations. To discriminate among the other alternatives, additional relocations of animals with large home range estimates would need to be collected to determine whether these animals' movements occur in a large circumscribed area or randomly in the river.

It is likely that home range size in these turtles depends more strongly on ecological (e.g., resource distribution) than ethological factors (e.g., dominance relationships). If this is the case, home range estimates must be qualified with reference to habitat. Practically, this necessitates home range estimates from many populations sampling the full extent of the species' habitat distribution. If ethological factors are also important, then ecological variables influencing quantity and quality of encounters, such as population density and sex ratio, must also be measured.

Overlapping home ranges occur in many emydid turtles (reviewed in Bury, 1979). This is not surprising since territoriality appears relatively uncommon in semi-aquatic members of the family (but see Lardie, 1983). However, there is evidence for dominance

hierarchies in captive animals (Harless, 1979), suggesting that in nature there may be non-exclusive use of some resources within a home range.

The estimated number of conspecifics encountered for *Pseudemys nelsoni* from this study appears sufficiently small for a social system based on individual discrimination to be functional. To demonstrate that turtles do individually recognize others in the field using observational techniques alone would be difficult given the problems associated with collecting a sufficiently large data base using underwater techniques. If it were known what resources could be monopolized by dominant animals, field experiments to unravel the social structure of this species might be realistic. Data on *P. floridana* were insufficient for conclusions; however, juveniles of this species performed as well, if not better, on the discrimination tasks discussed in Part 6.

The probability of recapture throughout an individual's home range is probably dependent on the distribution of resting areas (Florence and Murphy, 1976; see Don and Rennolls, 1983, for a similar conclusion about small mammals). Animals were most likely to be found near the banks in areas with places that an animal could rest with its head above water, especially if there was overhanging vegetation from the bank (Fig. 10). This is probably why one area of the study site was so well frequented, since both factors and basking sites were present over a 200 m distance. Even there, turtles were unlikely to be found in discontinuities in the supporting or overhanging vegetation. These observations of preferred microhabitat are consistent with those proposed by Sexton (1959) for painted turtles (*Chrysemys picta*), adjusting for the larger body size of *Pseudemys nelsoni*.

LITERATURE CITED

Anderson, T.W. 1982. The home range: A new nonparametric estimation technique. Ecology 63, 103-112.

Auth, D.L. 1975. Behavioral ecology of basking in the yellow- belled turtle, *Chrysemys scripta scripta* (Schoepff). Bull. Fla. State Museum Biol. Sci. 20, 1-45.

Begon, M. 1979. Investigating animal abundance: Capture-recapture for biologists. Univ. Park Press, Baltimore. 97 pp.

Bury, R. B. 1979. Population ecology of freshwater turtles. *In* M. Harless and H. Morlock (Eds.), Turtles: Perspectives and Research. John Wiley & Sons, N.Y. Pp. 571-602.

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939, 170-173.

Damuth, J. 1981. Home range, home range overlap, and species energy use among herbivorous mammals. Biol. J. Linnean Soc. 15, 185-193.

Don, B.A.C. and K. Rennolls. 1983. A home range model incorporating biological attraction points. J. Anim. Ecol. 52, 69-81.

Florence, T.H., Jr. and G.H. Murphy. 1976. A telemetric study of the activity of the red-eared turtle, *Chrysemys scripta elegans*. J. Tennessee Acad. Sci. 51, 60.

Ford, R.G. and D.W. Krumme. 1979. The analysis of space use patterns. J. Theor. Biol. 76, 125-155.

Harless, M. 1979. Social behavior. *In* Harless, M. and H. Morlock (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, N.Y. Pp. 475-492.

Jackson, D.R. 1988. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. Bull. Florida State Mus. Biol. Sci. 33, 113-158.

Jorgensen, C.D. 1968. Home range as a measure of probable interactions among populations of small mammals. J. Mammol. 49, 104-112.

Jorgensen, C.D. and W.W. Tanner. 1963. The application of the density probability function to determine the home ranges of *Uta stansburiana stansburiana* and *Cnemidophorus tigris tigris*. Herpetologica 19, 105-115.

Lardie, R.L. 1983. Aggressive interactions among melanistic males of the red-eared slider, *Pseudemys scripta elegans* (Wied). Bull. Oklahoma Herpetol. Soc. 8, 105-117.

MacCulloch, R.D. and D.M. Secoy. 1983. Movement in a river population of *Chrysemys picta bellii* in southern Saskatchewan. J. Herpetol. 17, 283-285.

Mahmoud, I.Y. 1969. Comparative ecology of the Kinosternid turtles of Oklahoma, Southwest Nat. 14, 31-66.

Marchand, L.J. 1945. The individual range of some Florida turtles. Copeia 1945, 75-77.

Morreale, S.J., J.W. Gibbons and J.D. Congdon. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). Canadian J. Zool. 62, 1038-1042.

Pearse, A.S. 1923. The abundance and migrations of turtles. Ecology 4, 24-28.

Plummer, M.V. and H.W. Shirer. 1975. Movement patterns in a river population of the softshell turtle, *Trionyx muticus*. Occas. pap. Mus. Nat. Hist., Univ. Kansas 43, 1-26.

Polis, G.A., C.N. McReynolds, and R.G. Ford. 1985. Home range geometry of the desert scorpion *Paruroctonus mesaensis*. Oecologia 67, 273-277.

Samuel, M.D., D.J. Pierce, and E.O. Garton. 1985. Identifying areas of concentrated use within the home range. J. Anim. Ecol. 54, 711-719.

Sexton, O.J. 1959. The spatial and temporal movements of a population of the painted turtle, *Chrysemys picta marginata* (Agassiz). Ecol. Monogr. 29, 113-140.

Southwood, T.R.E. 1966. Ecological methods. Methuen, London. 391 pp.

Swihart, R.K. and N.A. Slade. 1985. Testing for independence of observations in animal movements. Ecology 66, 1176-1184.

APPENDIX

TABLES AND FIGURES

Table 1. Sample sizes of *Pseudemys nelsoni* and *P. floridana* used to construct population utilization distributions.

Group	Figure	No. of individuals	No. of relocations	No. of pairs of relocation distances
male *Pseudemys nelsoni*				
with basking sites	5	46	216	634
without basking sites	6	37	119	186
female *Pseudemys nelsoni*				
with basking sites	5	34	156	492
without basking sites	6	29	89	122
male and female *P. nelsoni*				
without basking sites	8	66	208	308
male and female *P. floridana*				
without basking sites	9	19	54	57
Subgroups				
male *P. nelsoni*				
1.	7	15	41	42
2.	7	8	28	44
3.	7	13	39	45
4.	7	1	11	55
female *P. nelsoni*				
1.	7	9	27	39
2.	7	14	39	42
3.	7	6	23	41

Table 2. Sample sizes and data summary of all mark-relocations of *Pseudemys nelsoni* and *P. floridana* at Rock Spring run, Apopka, Orange Co., Florida, using maximum linear distance over water between relocations.

	Number of relocated individuals†	Number of relocations		Home range size	
		Mean	range	Mean	range
P. floridana					
males	7	2.6	2-5	355	0-684
females	12	3.9	2-6	242	0-630
P. nelsoni					
males	46	4.7	2-17	128	0-720
females	34	4.6	2-16	199	0-972

†Total numbers of *P. floridana* tagged are: Males, 21; females, 18. Total numbers of *P. nelsoni* tagged are: Males, 74, females, 52.

Table 3. Observed and expected frequencies to test the hypothesis that basking relocations are more likely to be located near the up- or downstream home range (HR) edge (G = 0.22, NS, 1 df).

Frequency	basking site at HR edge	basking site not at HR edge
Observed	21	11
Expected	19.7	12.3

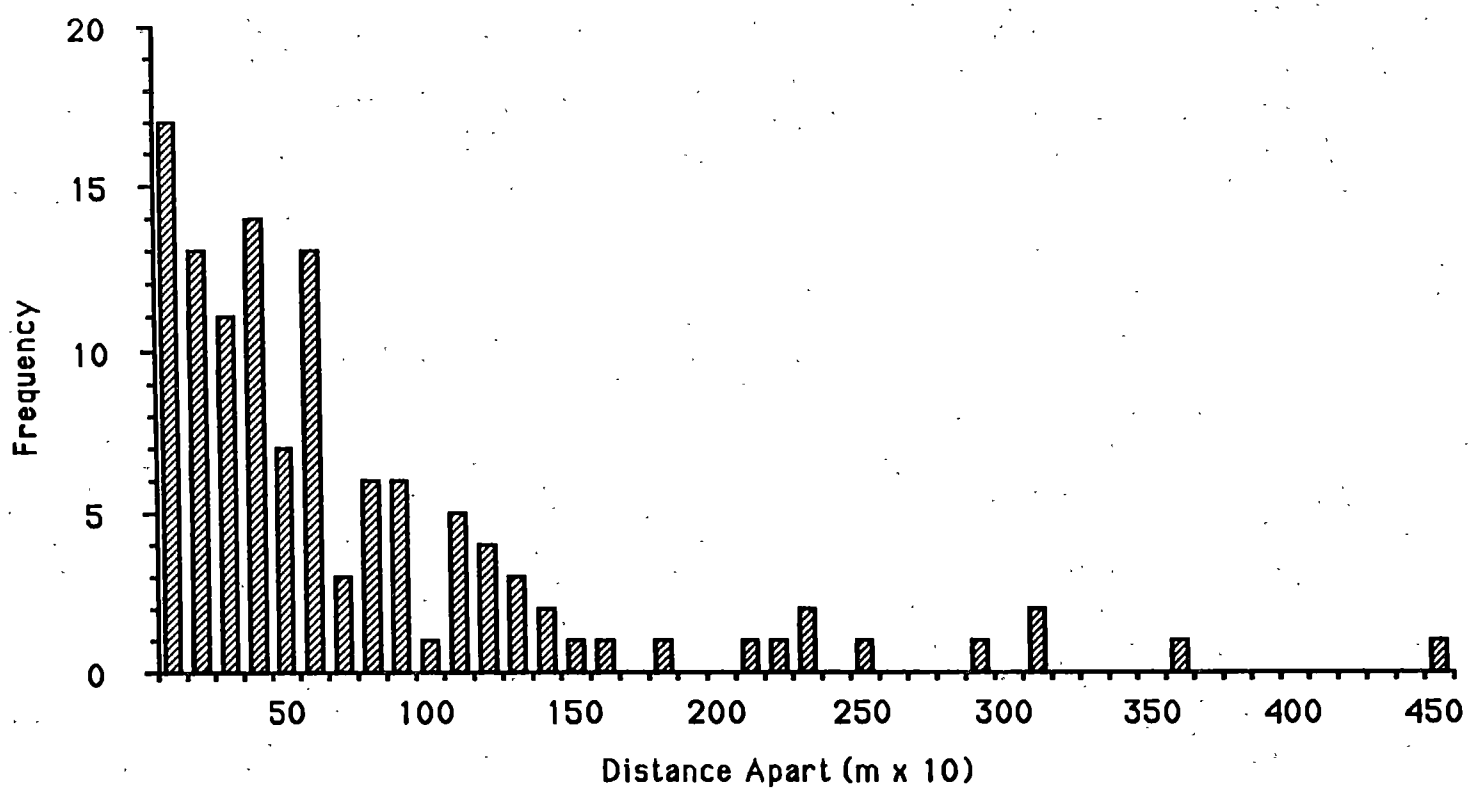

Figure 1. Frequency distribution of relocation distances of male *Pseudemys nelsoni* from Rock Springs run, Apopka, Orange Co., Fla.

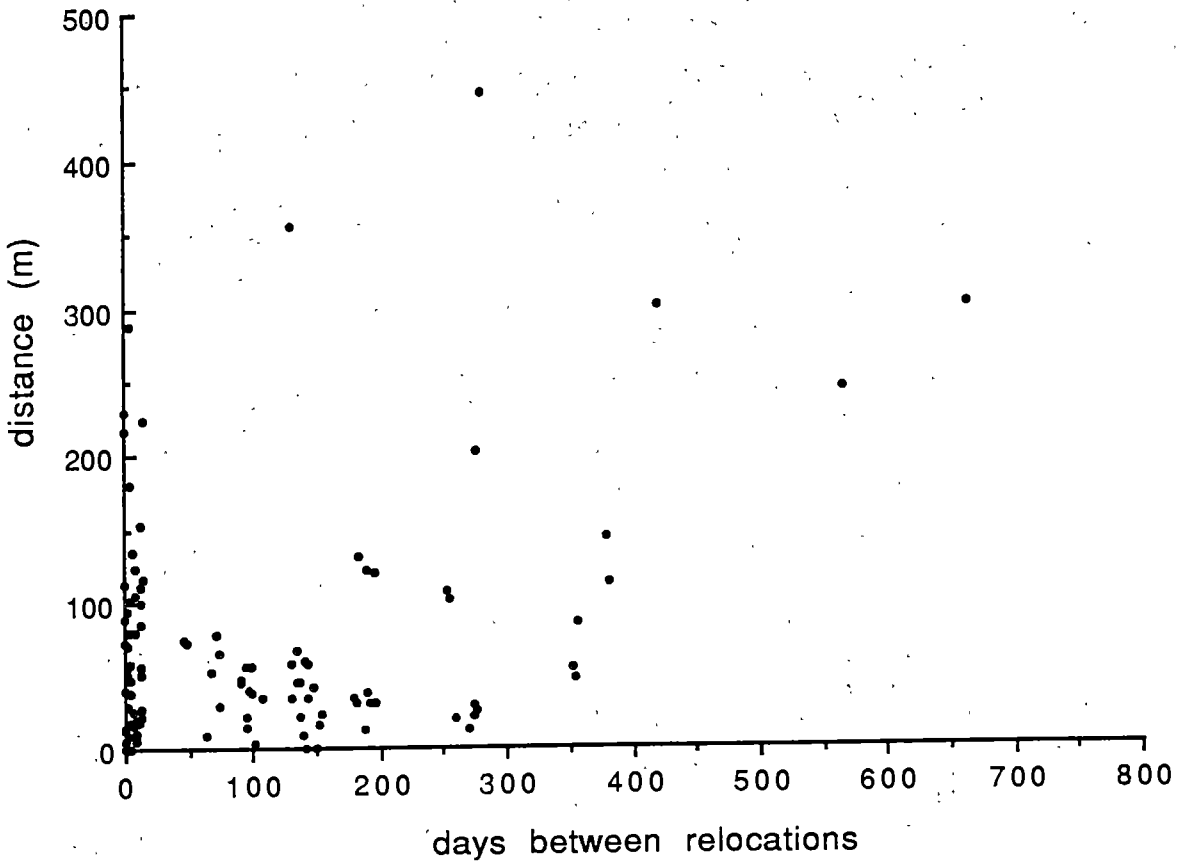

Figure 2. Scatterplot of the number of days between relocations and number of m between relocations for male *Pseudemys nelsoni* from Rock Springs run, Apopka, Orange Co., Fla. The correlation between these two variables is 0.33 (n = 118, NS).

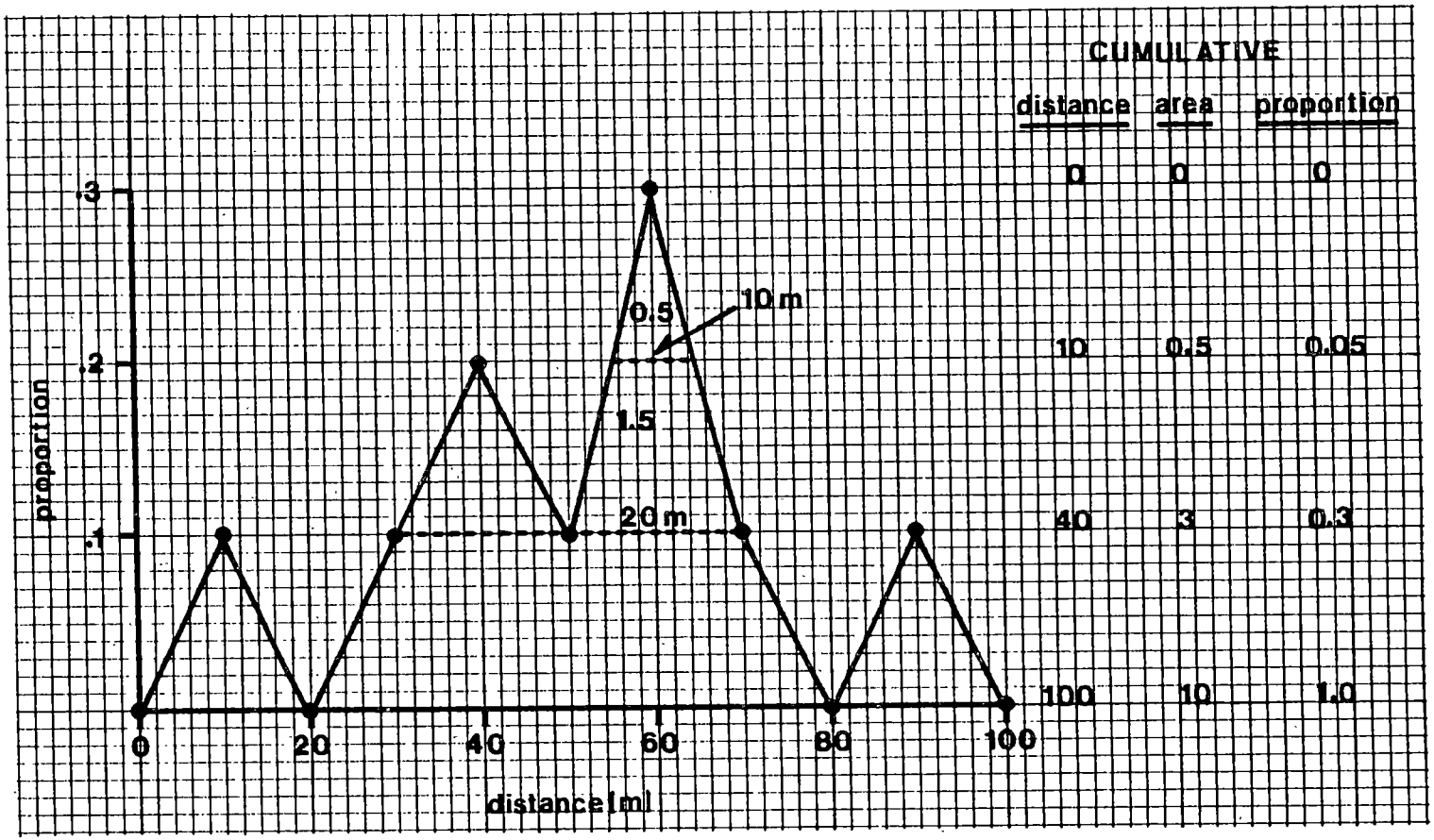

Figure 3. An example of how minimum distance (m) and proportion were calculated for Figures 7, 8b, and 9b.

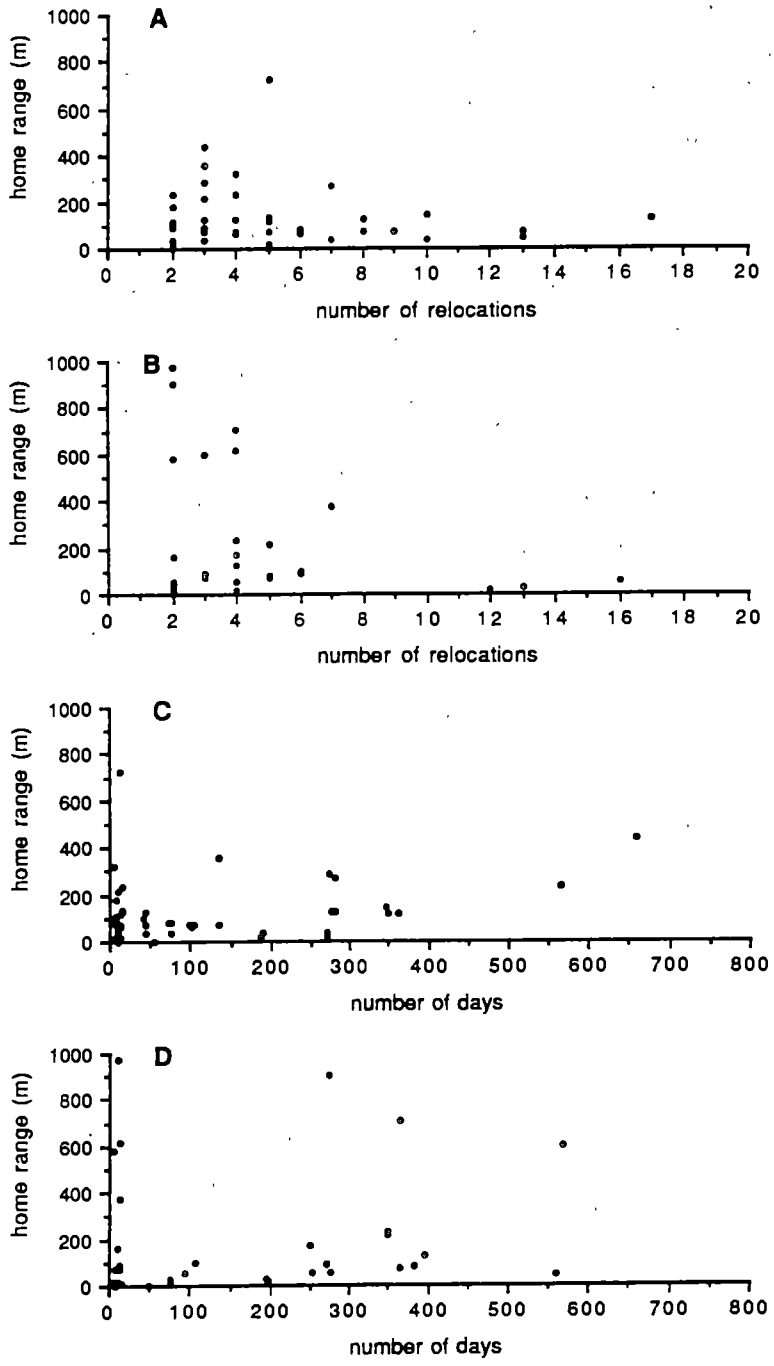

Figure 4. Scatterplots of home range length (linear distance over water) of male and female *Pseudemys nelsoni* from Rock Springs run, Apopka, Orange Co., Fla., and two possible explanatory variables. The maximum number of days between relocations of each individual. A. Males ($p > 0.25$, NS). B. Females ($p > 0.25$, NS). The number of relocations for each individual. C. Males ($p > 0.25$, NS). D. Females ($p > 0.25$, NS).

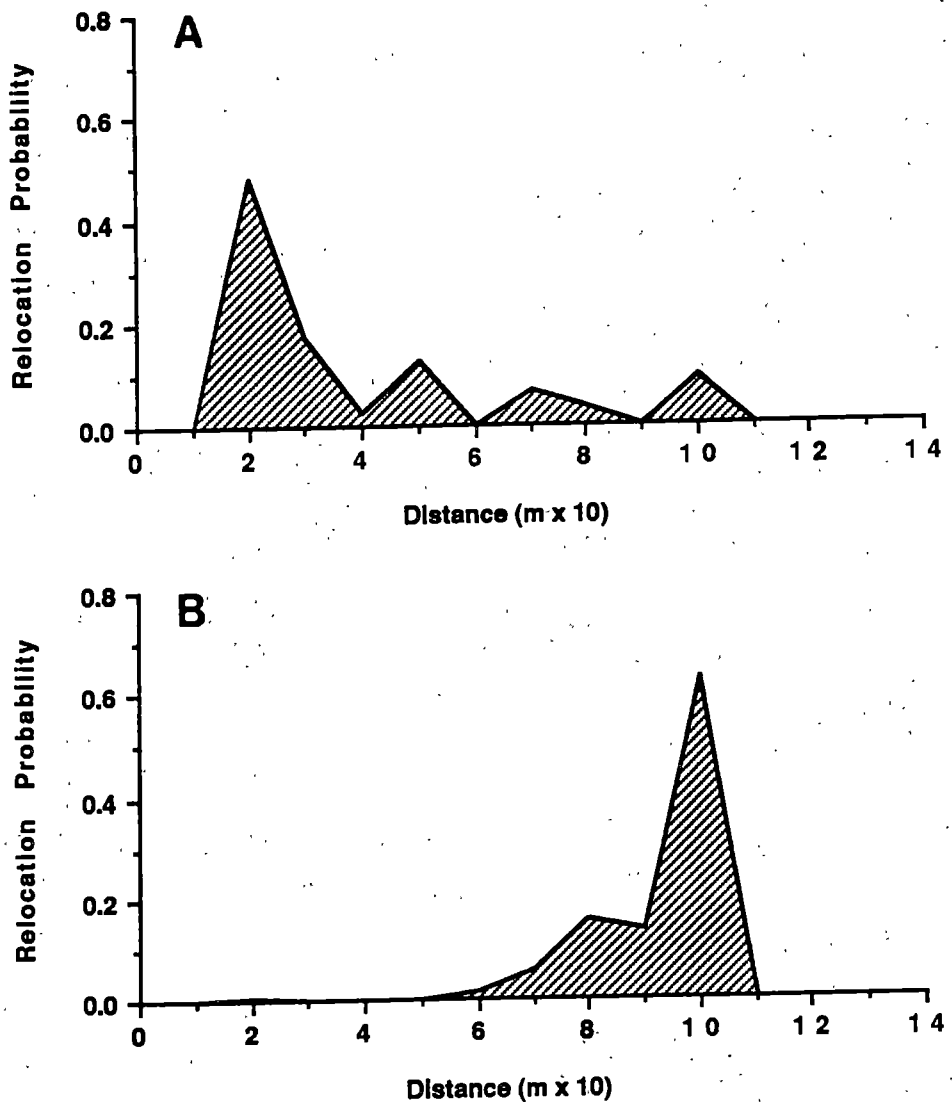

Figure 5. Population utilization distributions of *Pseudemys nelsoni* from Rock Springs run, Apopka, Orange Co., Fla., including basking relocations. A. Males. B. Females. The left-right orientation is arbitrary on these and other illustrations of population utilization distributions.

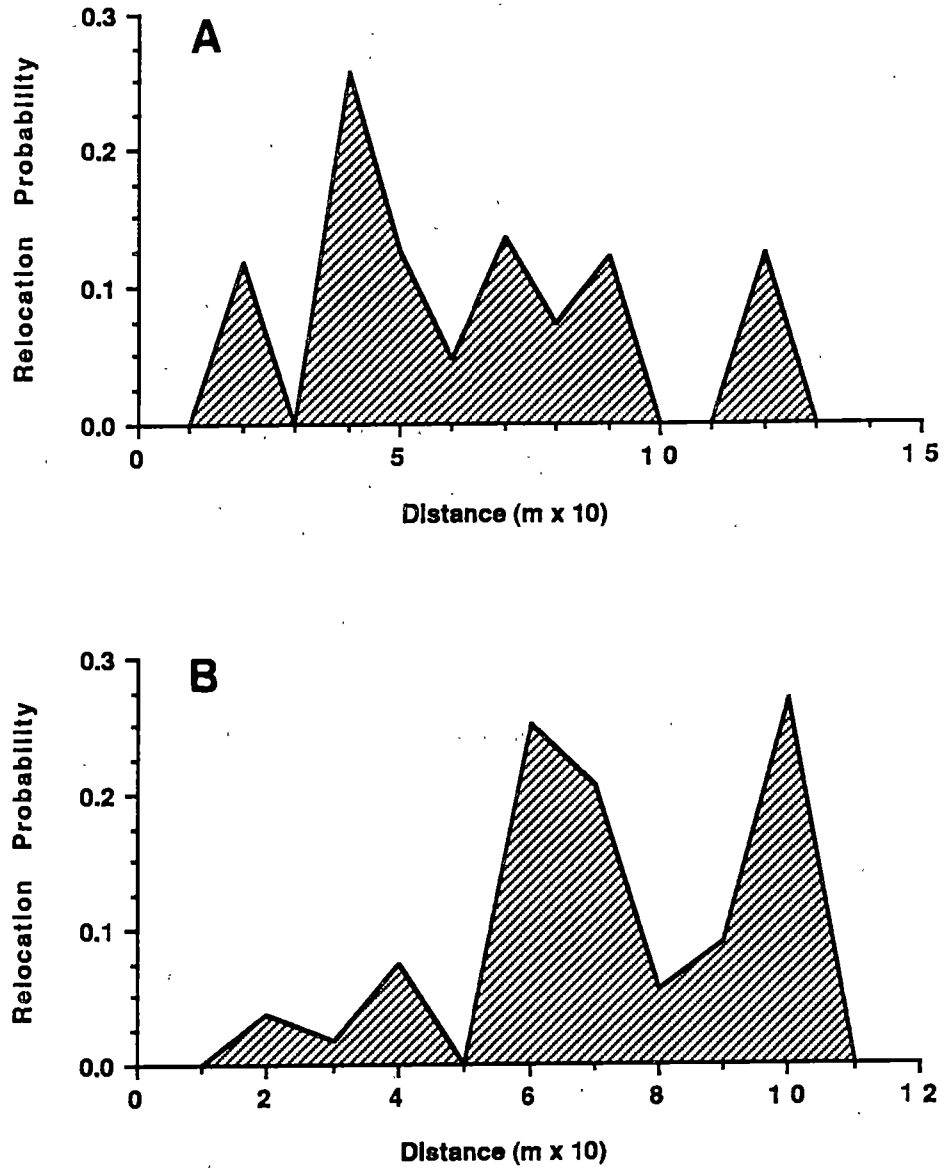

Figure 6. Population utilization distributions, without basking relocations, of *Pseudemys nelsoni* from Rock Springs run, Apopka, Orange Co., Fla. A. Males. B. Females.

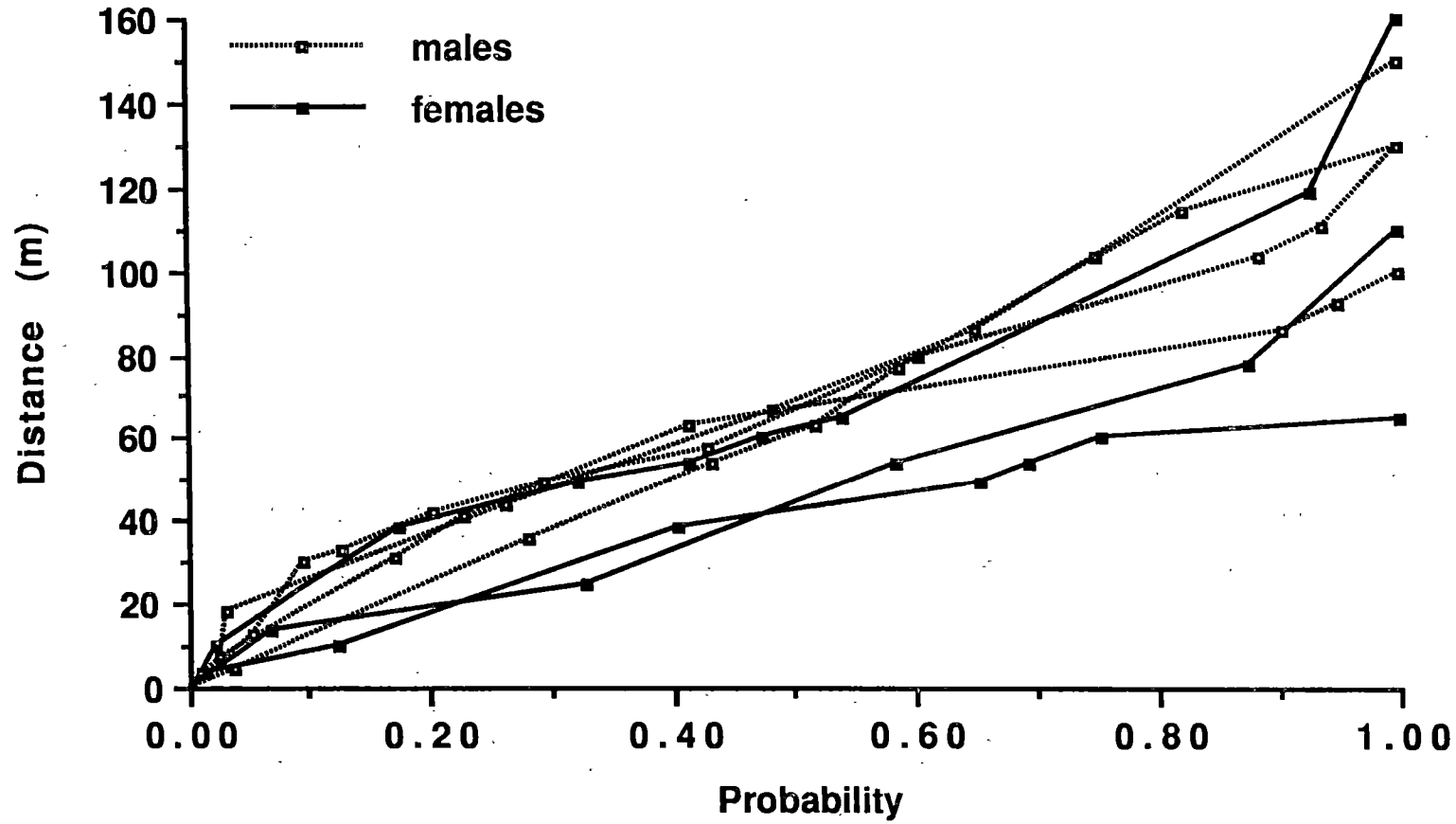

Figure 7. Minimum distance vs. probability plots for four subgroups of male and three of female *Pseudemys nelsoni*. See Table 2 for sample sizes.

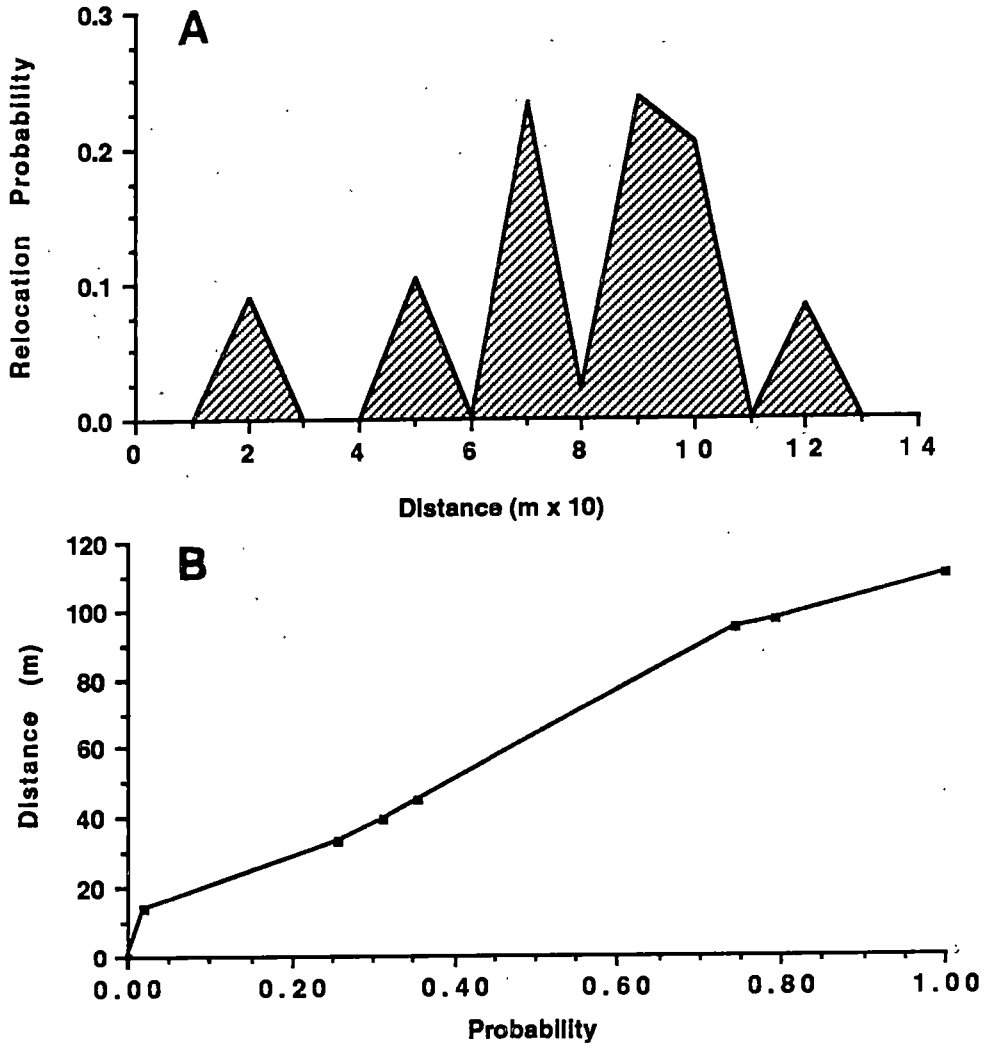

Figure 8. Population utilization distribution (A) and minimum distance vs. probability plots (B), without basking site relocations, of male and female *Pseudemys nelsoni* combined from Rock Springs run, Apopka, Orange Co., Fla.

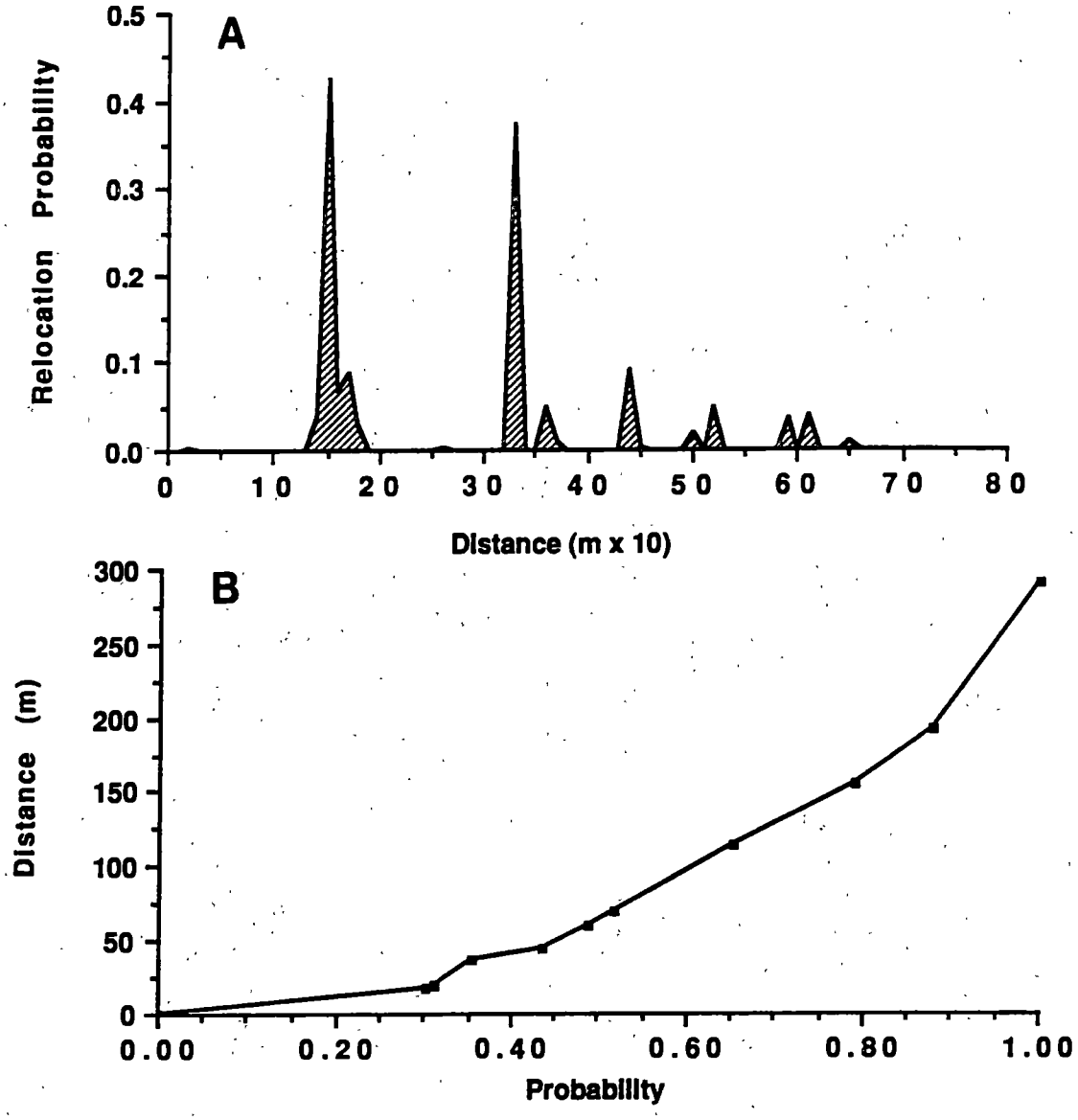

Figure 9. Population utilization distribution (A) and minimum distance vs. probability plot (B), without basking site relocations, of male and female *Pseudemys floridana* combined from Rock Springs run, Apopka, Orange Co., Fla. Minimum distance is calculated without including corridors, regions of the home range with zero probability of relocation.

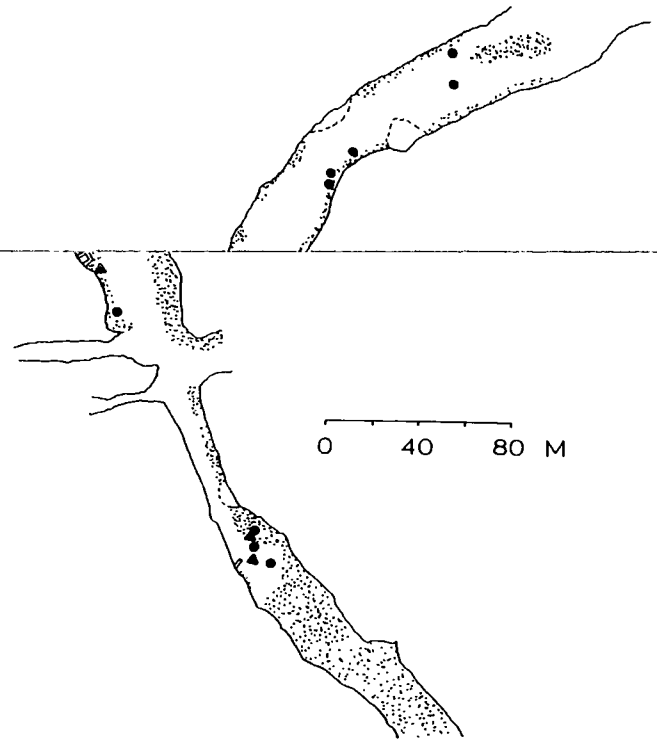

Figure 10. A map of the Rock Springs run study site, Apopka, Orange Co., Fla., indicating captures and relocations of male and female *Pseudemys nelsoni*. Not shown are 41 relocations of male and 25 of female *P. nelsoni*, and microhabitat features in areas with many relocations.

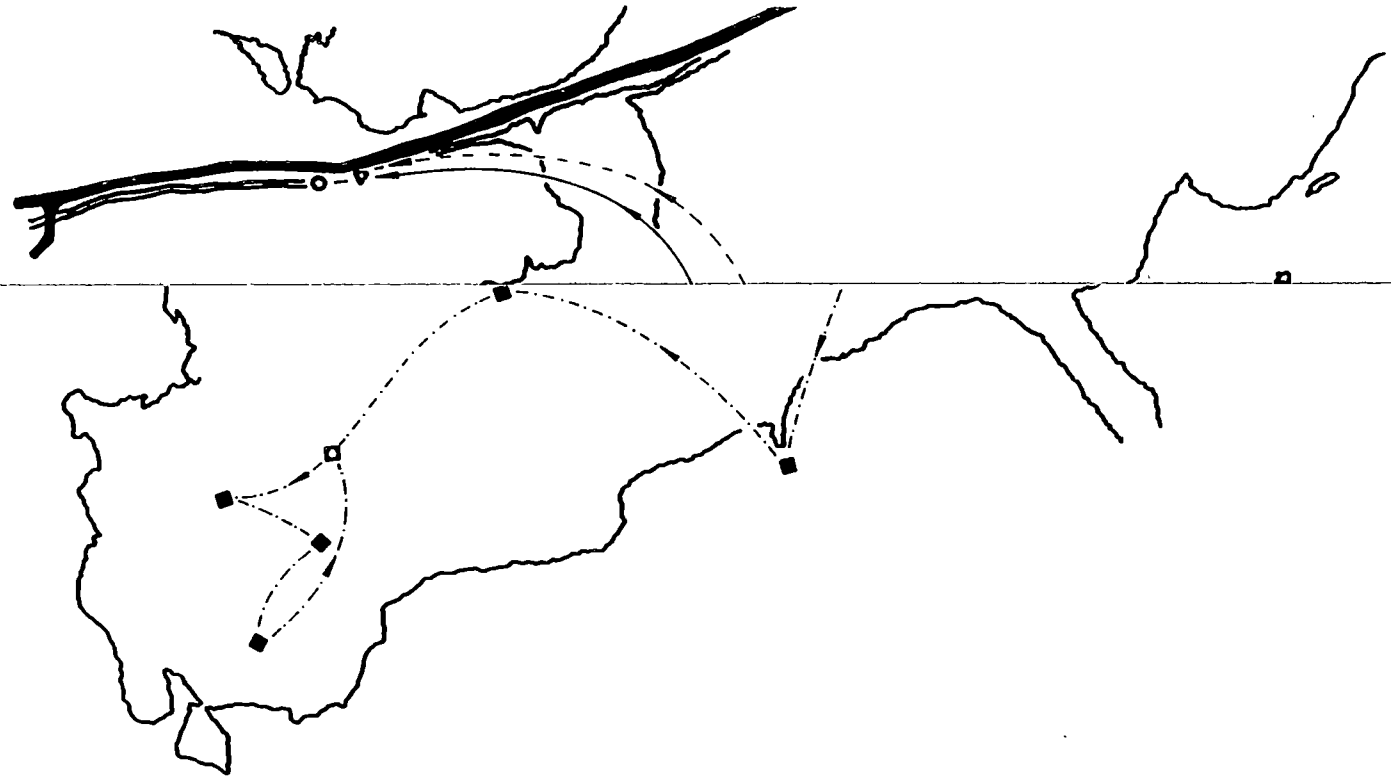

Figure 11. A map of the Payne's Prairie, Alachua Co., Fla., study site with relocations of three radiotracked *Pseudemys nelsoni*. Relocations of the male are given by a square symbol, those of females by a circle or square. Open symbols are initial capture/release points or final relocation points.

PART 8

SUMMARY

CHAPTER 1

SUMMARY OF PARTS 2 - 7

This project investigated the behavior and ecology of *Pseudemys nelsoni*, the Florida red-bellied turtle. *Pseudemys nelsoni* was chosen because it is abundant in some of the clear spring runs in Florida, the only feasible sites for observing these turtles under natural conditions. They are also easy to maintain in the laboratory in large aquaria or wading pools.

Three major objectives were considered in this study: To describe overt behaviors of free-ranging individuals, make a detailed analysis of selected behaviors and behavior sequences, and determine movement patterns of marked individuals. Field work was conducted in 1983-1986 to gather data on social behavior by direct, underwater observation (Rock Springs run, Apopka, Florida) and home range using mark-recapture and telemetry techniques (Rock Springs run and Payne's Prairie, Gainesville, Florida). Laboratory observations and experiments were conducted at the University of Tennessee in 1982-1986.

A behavior catalog of the Florida red-bellied turtle, *Pseudemys nelsoni*, was constructed based on 100 h of underwater field observations and supplemented by direct observations, Super-8 films, and videos of animals in the lab. Ninety-four aquatic, basking and emotional behaviors are described and placed in the context that they typically occur. Animals were inactive much of the time, often resting near the surface in small groups in a patch of debris or vegetation near the river bank. Foraging was solitary. Approaches and investigatory behaviors, performed mostly by males, were usually directed to conspecifics rather than syntopic *P. floridana*. Animals avoided facing others directly

except in agonistic encounters. Aggressive behavior, to other males and females, was rare and initiated by melanistic (dark) males. Fights among males ended abruptly, were of short duration, and often did not yield clear winners and losers. These aggressive interactions are consistent with a social structure based on a dominance hierarchy. In male-female aggressive behavior, a female was bit by a male on a forelimb, dragged to the bottom, tugged on, then released after several minutes. The function of this behavior is unknown. Males observed to court females were usually smaller than average and not strongly melanistic. Males of both species courted only conspecific females, suggesting that the lengthy courtship functions to initiate female receptivity rather than serve as an aid in species identification. Basking was a nonsocial activity, groups formed due to limited basking sites. Interactions during basking were infrequent, most behaviors observed were comfort and repositioning movements. Emotional behaviors included fear, anger/annoyance and pleasure. A fourth category, nonspecific arousal, may not be an emotional behavior, but was a clearly distinguishable motivational state. Social behavior is adapted for conditions of low visibility; olfactory cues appear to be important and long distance signals lacking. In this respect, animals did not take advantage of the clear water conditions at this spring run. Data were also taken on *P. floridana*. Their behavior was similar to that of *P. nelsoni* except for the absence of agonistic behavior. The behavior of *P. nelsoni* is compared to the behavior of related turtles drawn from the literature.

Behaviors of four juvenile *Pseudemys nelsoni* maintained in a large aquarium were recorded using checksheets to explore various techniques to detect patterns in behavior sequences and time. While there was significant individual variation among the juveniles, the analyses revealed that behaviors were assembled similarly by them. Most common were alternating pairs of behaviors, of these swimming and surfacing (to breathe) were especially frequent. Strong statistical relationships among behaviors were found for every

observation period; however, these relationships differed among observation periods. To an observer, the behavior of these turtles appears less organized than demonstrated by statistical analysis. The most useful techniques in this study were (1) identifying the most common sequentially linked behaviors, (2) a first order Markov chain analysis, (3) information theory techniques to estimate the average number of behaviors linked together, and (4) auto- and cross-association techniques to examine relationships among behaviors in time and variation among observation periods.

Posture changes and other behaviors of basking turtles were recorded for 43 h at Rock Springs run. Animals held their rear legs extended more often the longer they had been basking. Before testing frequencies of behaviors against null hypotheses of no change with time, it was necessary to establish the validity and power of the G-test for these data. Results of computer simulations demonstrated that the G-test was valid only for testing the behaviors of walks, turns, and extend legs. The null hypotheses for all three behaviors were rejected, movements are not independent of time. Walks and turns occur most frequently at the beginning of a basking session, following emergence; extending legs was most frequent from 15 - 45 min following emergence. Basking phases described for the yellow-bellied slider, *Trachemys scripta*, were not clearly discernable in *P. nelsoni*.

Precocial courtship was a frequent social event of juveniles maintained in the laboratory. Individuals were selective in their choice of partners and both sexes exhibited the behavior. There were a number of differences between precocial and adult courtship including posture, behavior sequences, role exchange, and absence of a consummatory act. The energetic nature of precocial courtship suggests that it should have an obvious function; however, none could be identified. Characteristics of this behavior coincide with those given for play, the function of which is also elusive.

Individual recognition abilities may influence the social organization of animals. The results of two laboratory experiments, one using positive reinforcement and the second punishment, suggest that both *Pseudemys nelsoni* and *P. floridana* can distinguish between a pair of turtles matched for size and pattern. This is consistent with observations of individuals interacting in the field.

Mark-relocation data of 80 *Pseudemys nelsoni* and 19 *P. floridana* from Rock Springs run were used to determine home range size and probability of relocation within a home range. The data were recast as a constrained nonlinear optimization problem and solved using a FORTRAN program. *P. nelsoni* was found to have the smaller home range with a minimum estimate of 120 m of river length, with most of the home range utilized. The home range estimate of *P. floridana* was 650 m with a patchier usage. Three radio-tracked *P. nelsoni* in a shallow lake in Payne's Prairie moved greater distances than most at Rock Springs run but still restricted themselves to a small portion of the lake and neighboring canal. In both study sites, the entire home range could be traversed by an individual in one or two hours.

VITA

Matthew Kramer was born on 30 May 1953 in New York City. He grew up in Bergenfield, N.J. where, encouraged by his parents, he developed an avid interest in reptiles and amphibians. He graduated in 1975 from Cook College, Rutgers University, with a B.S. in Wildlife Biology. After moving to Colorado, he joined a collective that operated a natural foods restaurant. In the ensuing years he traveled and worked odd jobs in various parts of the United States and Europe, ending up in Amsterdam. There he worked as a local musician and met Catherine Auvraud, his future wife. He lived in France for a year, then traveled through northern and equatorial Africa. He and Catherine were married in Kenya, where they taught high school, in 1980. He entered the Ph.D. program in Zoology at the University of Tennessee in 1981. His current favorite guitarist is Jim Hall.