TURTLE NEST SENSORY PERCEPTION
BY
RACCOON (*Procyon lotor*) AND STRIPED SKUNK (*Mephitis mephitis*):
AN APPROACH THROUGH DISCRIMINATION LEARNING
OF POTENTIAL NEST CUES.

by

Patrick Galois

A Thesis

Submitted to the Faculty of Graduate Studies and Research

in partial fullfilment of the requirements for the degree of

Doctor of Philosophy

In the Department of Natural Resource Sciences,

McGill University, Montréal, Canada, May 1996.

® Patrick Galois, 1996

National Library
of Canada

Bibliothèque nationale
du Canada

Acquisitions and
Bibliographic Services

Acquisitions et
services bibliographiques

395 Wellington Street
Ottawa ON K1A 0N4
Canada

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-29941-4

Canada

Raccoon - from Algonquian "arathcone" meaning:
"he who scratches with his hands".
Webster's Dictionary. 2nd ed. 1961.

Skunk - from "segankw" or "segongw" of Abenaki Indian
(Algonquian linguistic family) meaning:
"he who urinates".
Webster's Dictionary. 2nd ed. 1961.

ABSTRACT

Egg predation may be the most important mortality factor for North American turtles. This predation can destroy 50-90% of nests in an area. The major predators are striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*). Despite differences in their habits and diet, these species appear equally efficient in turtle egg predation, even though these eggs represent a very small portion of their annual food intake. Sight, olfaction, touch and hearing could be used by these predators to find the nests. The aim of this study was to document intra and inter-specific differences in the perception of possible nest-cues used by raccoon and striped skunk. Choice-tests based on food-conditioning were carried out with two visual cues (dark and smooth surface), one olfactory cue (turtle urine) and one tactile cue (soil compaction). Subject performances (number of trials to obtain 80% success rate in the different tests) were compared to assess intra and inter-species, and skunk inter-age differences in sensory perception and learning abilities. As expected raccoons learned the tactile cue discrimination faster than the visual cue discriminations. The tactile cue discrimination was learned as fast as the olfactory cue. As expected skunks learned the olfactory cue discrimination faster than other cue discriminations. When compared, the olfactory cue appeared to be as important for both species even though raccoons had faster learning rates than skunks in all the tests except for one visual test. Juvenile skunks learned faster than adult skunks with four out of six juveniles performing better in the olfactory test. Olfaction may play an important role in nest localization by raccoons and skunks, and sight may also play a role for raccoons. Learning turtle nest cues while with their mother could facilitate their future ability in locating turtle nests.

RÉSUMÉ

La prédation des oeufs est un des facteurs de mortalité important chez les tortues en Amérique du Nord. Cette prédation peut entraîner une perte de 50 a 90% des nids. Les principaux prédateurs sont la mouffette rayée (*Mephitis mephitis*) et le raton laveur (*Procyon lotor*). Malgré quelques différences dans leur mode de vie et leur régime alimentaire, ces deux espèces semblent aussi efficaces dans la prédation des oeufs de tortue, ces oeufs ne représentant toutefois qu'une faible part de leur alimentation annuelle. La vue, l'olfaction, le toucher et l'ouïe serait utilisés par ces prédateurs pour trouver les nids. Cette étude avait pour but d'établir les différences dans la perception d'indices potentiels utilisés par le raton laveur et la mouffette. Des tests de choix basés sur le conditionnement alimentaire ont été menés avec deux indices visuels (surface sombre et lisse), un indice olfactif (urine de tortue), et un indice tactile (surface compactée). Les performances des sujets (nombre d'essais pour obtenir 80% de réponses correctes) ont été comparées aux niveaux intra et inter-spécifiques, et inter-âge (mouffette) de la perception sensorielle et des capacités d'apprentissage. Comme prévu, les ratons laveurs ont appris plus vite la discrimation tactile que les discriminations visuelles. La discrimination olfactive a été apprise aussi vite que la discrimination tactile. Les mouffettes ont appris plus vite la discrimination olfactive que les autres discriminations. L'indice olfactif a la même importance pour les deux espèces bien que la vitesse d'apprentissage ait été plus rapide pour les ratons dans tous les tests sauf un test visuel. Les jeunes mouffettes ont appris plus vite que les adultes, quatre des jeunes sur six performant le mieux dans le test olfactif comme les adultes. L'olfaction aurait donc un rôle primordial dans la localisation des nids de tortue par les ratons laveurs et les mouffettes, et la vision pourrait aussi jouer un certain rôle pour les ratons laveurs. L'apprentissage des indices dans la recherche de nids de tortues serait facilité chez les jeunes mouffettes. Ainsi la période pendant laquelle les jeunes accompagnent leur mère pourrait être des plus favorable pour l'apprentissage de la localisation des nids de tortues.

ACKNOWLEDGEMENTS

Many people have contributed significantly to this work in many ways. First, I would like to thank my family and particularly my parents who supported me (morally and financially) these past years despite some uncertainty of the outcome. Everything started with the precious help of Mme Véronique Derguy-Tremblay and the Abbé Jean-Marie Potvin who prospected for a supervisor. I am also grateful for their wonderful welcome to Québec.
J. R. Bider, my supervisor, who accepted me without knowing me and for his inspiring discussions, support and patience with my poor English. I would like to thank Fred Whoriskey for his advice and for reviewing my thesis. I would like to thank Joël Bonin for his support, advice and friendship and for my initiation to the realm of amphibians and reptiles, and Simon Nadeau for his friendship and advice. I thank both for the opportunities they gave me to enjoy the Canadian wilderness. The staff of the Ecomuseum Anne Bérubé, Debbie Roffe, Derek Delutis, Sylvie Matte, Stéphane Poulin, and Richard Van Ingen, for their help and friendship, even accepting to take some risks with my skunks. Mrs Lynn Miller and Mr Beaumont who provided some of the animals. Finally, a big "Danke schön" to Susanne Vogelsgang who kindly translated the german scientific papers.

Part of the funding was provided by N.S.E.R.C. research fund and a McGill Summer Bursary. The St-Lawrence Valley Natural History Society provided me with all the facilities needed to keep the animals and to conduct my research at the Ecomuseum .

PREFACE

This thesis is presented in traditional thesis format. It consists of a short introduction, a literature review, a materials and methods section and four chapters presenting the results and their discussion. The thesis ends with a general discussion and conclusion. A list of references cited and appendixes presenting raw data are provided.

This dissertation is in accordance with the Guidelines concerning Thesis Preparation as published by the Faculty of Graduate Studies and Research of McGill University which states:

> "Candidates have the option of including, as part of the thesis, the text of a paper(s) submitted for publication, or the clearly-duplicated text of a published paper(s). These texts must be bound as an integral part of the thesis.
>
> If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.
>
> The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: A Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a comprehensive review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.
>
> Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.
>
> In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest of the accuracy of such statements at the

> doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers. Under no circumstances can a co-author of any component of such a thesis serve as an examiner for that thesis."

All the work involved in the present thesis was the responsibility of the candidate. Professor J.R. Bider was thesis supervisor. Professor F. Whoriskey participated in the editing of this document.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDIXES

CLAIM OF CONTRIBUTION TO KNOWLEDGE

1. This study was the first to compare two important turtle nest predators, raccoon and striped skunk, using the same experimental protocol to assess through behavioral responses the perception of potential turtle nest cues.

2. This is also the first time that sensory perception of potential turtle nest cues was investigated in the laboratory using food-conditioning. Four different cues were tested separately and involved the use of sight, olfaction or touch.

3. The experimental protocol and apparatus were designed in order to avoid the use of invasive techniques and could easily be adapted to other turtle nest predators such as mink, fox or coyote.

4. The results of nest cue discrimination tests indicated that raccoons learned tactile cue discrimination as fast as olfactory cue discrimination and visual contrast dark/light discrimination for some subjects. The best performances obtained by skunks were in the olfactory test as predicted. Therefore olfaction might play an important role for both species in turtle nest localization.

5. Raccoons learned faster than skunks in all the tests except in the visual texture test in which both species performed equally poorly.

6. Juvenile skunks learned faster than adults but like the latter tended toward a better performance in the olfaction test. This rapid learning ability of young while they accompany their mother is thought to be of particular advantage when foraging in turtle nesting areas where indirect nest cues must be learned.

I. INTRODUCTION

Turtle nest predation is of concern because human activities often exacerbate this natural ecological process. Turtle conservation programs have been implemented, but with variable success in part because some incompletely answered questions persist about the nest localization ability of the predators (Burger 1977; Wilhoft et al. 1979; Snow 1982). Methods aimed at total removal or extermination of problem predator species are unpopular and unwise (McCabe and Kozicky 1972; Davis and Whiting 1977; Sargeant et al. 1984; Congdon et al. 1994). In the case of nest predation, understanding a predator's foraging behavior may lead to effective conservation programs for both prey and predators. The aim of this project was to assess the sensory perception of potential nest cues by raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*), the principal predators of turtle nests in North America (Hammer 1969; Congdon et al. 1983; McMurtray 1986; Robinson and Bider 1988). I used discrimination-learning based on food-conditioning. This allowed me to analyze separately potential visual, olfactory and tactile cues. Captive wild raccoons and striped skunks were submitted to these discrimination tests allowing intraspecific (Chapter V and VI) and interspecific (Chapter VII) comparisons of the cues and senses used to find nests, as well as learning abilities. In 1993, the birth of skunks in captivity gave me the opportunity to investigate the influence of age and experience on the learning abilities in sensory discrimination (Chapter VIII). The general discussion and conclusion emphasize the possible importance of olfaction and learning in turtle nest predation and the implications in nest protection programs.

II. LITERATURE REVIEW

1 TURTLE NEST PREDATION

For millions of years, turtle populations have successfully coped with nest predation, one of their important natural mortality factors. Unfortunately, recent human activities seem to be having direct and indirect impacts on turtles. By altering and destroying natural habitats, urbanising lake, river and sea shores, drying wetlands, polluting water, and collecting eggs and adults, man, in a few decades, has introduced new mortality factors in addition to predation. Worse yet, habitat alteration, especially through agriculture, has also favored turtle nest predators (Stancyk 1982; Congdon et al. 1993). Opportunistic raccoons have profited from abundant crops, mainly corn (*Zea mays*) (Yeager and Rennels 1943; Yeager and Elder 1945; Shoonover and Marshall 1951; Dorney 1954; Ellis 1964; Shirer and Fitch 1970; Sonenshine and Winslow 1972; Rivest and Bergeron 1981; Dunn and Chapman 1983; Traversy et al. 1989; Taulman and Williamson 1994). In this modified environment, nest predation could have a dramatic impact on some reduced turtle populations (Congdon et al. 1993). Thus it is not surprising that turtle nest predation has become a concern among herpetologists (Stancyk et al. 1980; Hopkins and Murphy 1982; Nicolaus et al. 1982; McMurtray 1986; Conover 1989). Predation varies greatly and can destroy from 2.1%-99% of the nests in an area (Hammer 1969; Burger 1977; Davis and Whiting 1977; Landers et al. 1980; Petokas and Alexander 1980; Tinkle et al. 1981; Snow 1982; Congdon et al. 1983, 1987; Ernst 1986; McMurtray 1986; Christens and Bider 1987; Robinson and Bider 1988; Linck et al. 1989), increasing the risk of decline of turtle populations (Gibbons 1968; Iverson 1991; Congdon et al. 1993, 1994) (Table 2.1).

2 ANTI-PREDATION METHODS

Several methods have been used to reduce predation on both turtle and waterfowl nests. The tasks are similar: protecting static and generally inconspicuous objects. These methods were used

Table 2.1. Predation rates of turtle nests for different turtle species in North America (rates are expressed in percentage of located nests destroyed).

Turtle species	Author(s)	Predation rate in %	Main predator
Painted turtle *Chrysemis picta*	Tinkle et al. (1981)	21	R
	Snow (1982)	40.7	S
	Christens and Bider (1987)	43.8	R
Snapping turtle *Chelydra serpentina*	Hammer (1969)	63	S-R
	Petokas and Alexander (1980)	94	R
	Congdon et al. (1987)	70 to 100	R
	Robinson and Bider (1988)	84.3	S
Blanding's turtle *Emydoidea blandingii*	Congdon et al. (1983)	67	R
Diamondback terrapin *Malaclemys terrapin*	Burger (1977)	51 to 71	R
Loggerhead turtle *Caretta caretta*	McMurtray (1986)	97-99	R

R=raccoon S=striped skunk

(After Iverson, 1991)

when managers were faced with high predation rates and declining prey populations. In many cases predator control was attempted but the use of systematic, live-trapping or kills over large areas were time consuming, difficult, and of limited success (Greenwood 1986; Crabtree et al. 1989). Moreover predator control was and is controversial, and its use difficult to justify in parks and natural reserves (McCabe and Kozicky 1972; Davis and Whiting 1977; Sargeant et al. 1984; Goodrich and Buskirk 1995). The controversy has escalated as the public and wildlife managers become more concerned with biodiversity and a global approach to conservation (Wilson and Peter 1988; Frazer 1992; Pimm and Gittleman 1992; Congdon et al. 1993, 1994; Angermeier and Karr 1994; Sinclair et al. 1995).

Other new approaches to solve excessive predation have been used. Turtle nests were individually protected with screens (Bleakney 1963; Landers et al. 1980; McMurtray 1986; Schwarzkopf and Brooks 1987; Congdon et al. 1994). Eggs have been collected and transplanted into a safe site soon after their laying (McMurtray 1986; Stancyk et al. 1980; Talbert et al. 1980) or artificially incubated (Ewert 1979; Bustard 1979; Bider, pers. comm.). This last method is efficient but involves intensive labor to monitor wild nesting. Furthermore the disturbance of the nests and gravid females, and the manipulation of the eggs can be deleterious (Bustard 1979; Ewert 1979; Talbert et al. 1980). The "head-starting" technique consists of raising hatchlings and was largely used in sea turtle conservation programs (Stancyk 1982; Frazer 1992). It was criticized by Ehrenfeld (1982) and Frazer (1992) who argued that the period of captivity might affect behavior, especially future nesting migrations (Bowen et al. 1994; Karl et al. 1995). Also the survival rate of released young when compared to that of their wild counterparts might be low, and their chance to reach adulthood might be less.

A method requiring little labor is to limit the access of predators to nesting sites using electric fences combined with predator live-trapping inside the fenced area and relocation program. This efficient technique is now popular in waterfowl nest protection (Lokemoen et al. 1982; Greenwood et al. 1990; Deblinger et al. 1992; LaGrange et al. 1995) and has been used successfully for turtles (Bider, pers. comm.).

Crabtree and Wolfe (1988) studied the use of an alternate food source to lure predators away from waterfowl nesting sites and succeeded in reducing egg predation by skunks but at the expense of compensatory predation by other mammalian predators, e.g. weasel (*Mustela erminea*) and red fox (*Vulpes vulpes*).

In a trial test chicken eggs were used for bait to assess the efficiency of a possible chemosterilizing campaign to reduce predator populations. This method appeared efficient for raccoons but not skunks because the bait was mostly distributed around wetlands, habitat highly used by raccoons but less by skunks (Nelson and Linder 1972).

Another approach to reduce nest predation is to modify the behavior of predators with food taste aversion conditioning. This method is not new (Gustavson 1974) but is gaining popularity, particularly in waterfowl management. Illness-inducing substances were injected in eggs displayed in a nesting area. Animals feeding on these eggs became ill for a short-term period, developing a general aversion toward eggs through association of egg taste and illness. Tests are now being carried out using non-toxic substances such as emetine (Conover 1989, 1990) or estrogen (Nicolaus et al. 1989a,b; Semel and Nicolaus 1992; R. Penner, pers. comm.) which are difficult to detect by smell or taste compared to the toxic lithium chloride previously used (Gustavson 1977; Hopkins and Murphy 1982; Nicolaus et al. 1982; Nicolaus 1987). Unfortunately this method failed to reduce nest predation of sea turtles in one study (Hopkins and Murphy 1982). It was suspected that the raccoons simultaneously consumed treated and non-treated eggs thus receiving some positive reinforcement that prevented the establishment of an aversive response.

The results of these methods remain unpredictable in part because of the lack of knowledge relating to foraging behavior and the sensory information used by the predators involved. In the late 1970's, the limited efficiency of the aversion method used to reduce livestock predation by coyotes (*Canis latrans*) eventually led to research on coyote sensory ecology (Wells and Lehner 1978; Wells 1978). Coyotes appeared to rely mostly on sight to locate prey, olfaction and audition having a complementary role, particularly in the dark. This information was considered to develop more effective aversive techniques for example by increasing the visibility of the baits.

Given present problems involving the turtle nest predation, field experiments and observations raised questions about the efficiency of the predators and their ability to find nests (Burger 1977; Wihloft et al. 1979; Snow 1982). The necessity to fill this gap in our knowledge caused a resurgence of interest in the study of nest predation (waterfowl and turtle) and the predator species involved (Nams 1991; Semel and Nicolaus 1992; Larivière, pers. comm. 1994; Tuberville and Burke 1994; Niemuth and Boyce 1995; Pasitschniak-Arts and Messier 1995). In addition to contributing to scientific knowledge, a better understanding of predation and cues used by these predators might help elaborate better turtle protection programs.

3 PREDATORS

In North America many species prey on turtle nests and sometimes on turtles. The list of turtle nest predators "is limited by the ingenuity in researchers' identification of predators rather than the ingenuity of the predators" (Burger 1977). The following predators reported in the literature attests to Burger's insight. They are: red fox (Hamilton 1940; Burger 1977; Snow 1982; Congdon et al. 1983, 1987; Linck et al. 1989; Macdonald et al. 1994), gray fox (*Urocyon cinereoargenteus*) (Landers et al. 1980; Congdon et al. 1983), mink (*Mustela vison*) (Hamilton 1940; Hammer 1969; Snow 1982), spotted skunk (*Spilogale putorius*) (Hammer 1969), chipmunk (*Tamias striatus*) (Snow 1982), opossum (*Didelphis virginianus*) (Landers et al. 1980; Temple 1987), human (*Homo sapiens*) (Davis and Whiting 1977; Robinson and Bider 1988; Congdon et al. 1994), crows (*Corvus brachyrhynchos*) (Burger 1977), gulls (*Larus* sp.) (Burger 1977); snakes (Legler 1954; Landers et al. 1980), and ants (Hammer 1969; Burger 1977).

The two most serious predators are the raccoon (*Procyon lotor*) (Hamilton 1940; Stuewer 1943; Yeager and Rennels 1943; Erickson and Scudder 1947; Cagle 1949; Llewellyn and Uhler 1952;

Hammer 1969; Burger 1977; Davis and Whiting 1977; Wilhoft et al. 1979; Landers et al. 1980; Petokas and Alexander 1980; Stancyk et al. 1980; Talbert et al. 1980; Hopkins and Murphy 1982; Snow 1982; Congdon et al. 1983, 1987; Ernst 1986; Christens and Bider 1987; Temple 1987; Robinson and Bider 1988; Linck et al. 1989; Farrell and Graham 1991; Tuberville and Burke 1994) and the striped skunk (*Mephitis mephitis*) (Hamilton 1940; Hammer 1969; Landers et al. 1980; Snow 1982; Congdon et al. 1983, 1987; Christens and Bider 1987; Robinson and Bider 1988).

These carnivores are sympatric in most of their range (Lotze and Anderson 1979; Wade-Smith and Verts 1982), including Southern Québec. They are both mainly nocturnal (Bider et al. 1968; Gauthier 1971). Raccoons eat a wide variety of plant and animal matter (Stuewer 1943; Yeager and Rennels 1943; Yeager and Elder 1945; Erickson and Scudder 1947; Hamilton 1951; Llewellyn and Uhler 1952; Dorney 1954; Hoffman and Gottshang 1977; Lotze and Anderson 1979; Rivest and Bergeron 1981; Sanderson 1987). Llewellyn and Uhler (1952) identified over one hundred animal items in raccoon stomachs and scats from a Maryland study site. Skunks also have a varied diet but prefer insects (Hamilton 1936; Kelker 1937; Llewellyn and Uhler 1952; Verts 1967; Shirer and Fitch 1970; Wade-Smith and Verts 1982). Raccoons preferentially use wetland, river and sea shores, as well as wooded areas (Stuewer 1943; Dorney 1954; Shirer and Fitch 1970; Urban 1970; Nelson and Linder 1972; Sanderson 1987; Fritzell 1978a; Greenwood 1982; Glueck et al. 1988; Kissel and Kennedy 1992) whereas skunks are found more often in open areas and fields (Shirer and Fitch 1970; Bailey 1971; Crabtree et al. 1989; Kennedy et al. 1991).

Despite these differences, both species seem very efficient in turtle egg predation even where this food item represents a very small portion of their annual food intake.

4 NEST VULNERABILITY

Different nest characteristics, nest distribution and environmental conditions could affect turtle nest vulnerability to predation.

4.1 Age of the nest

Most studies conclude that predation occurs during the nesting period. Most of the nest destruction occurs in the 48 to 72 hours following nesting, and predation rates decrease during egg incubation (Petokas and Alexander 1980; Tinkle et al. 1981; Congdon et al. 1987; Christens and Bider 1987; Robinson and Bider 1988). However, some authors reported a high level of predation during incubation. In Burger's study (1977), the rate was high during the nesting period, decreased and then increased at the end of incubation period. Snow (1982) observed a high rate of predation in the 4 days following nesting and a lower but constant predation rate for the next 18 days. On a nesting site located in Southern Québec which was used by four turtle species, no predation occurred during the nesting season. Later in the summer around hatching time predators were able to find and destroy 26 unprotected nests (per. obs. 1995).

4.2 Between nest distance

The dispersion of nests depends on turtle species (Ehrenfeld 1979) and on availability of suitable nesting sites (Ehrenfeld 1979; Obbard and Brooks 1980; Christens and Bider 1987). The clumped nests of some sea turtles is a typical example of a distribution which promotes heavy predation (Davis and Whiting 1977; Bustard 1979; Hopkins and Murphy 1982; McMurtray 1986). Hammer (1969) obtained a high positive correlation between snapping turtle nest densities on dikes and predation level. In a more recent study, snapping turtle nests within one meter of each other were more vulnerable to predation than those farther apart (Robinson and Bider 1988).

4.3 Distance from water

Nests situated less than 30 meters from water are more susceptible to raccoon predation (Christens and Bider 1987; Congdon et al. 1987). However, distance from water has no influence on nest vulnerability to skunk predation (Robinson and Bider 1988).

4.4 Vegetation cover

Temple (1987) observed an edge effect on predation rate, where nests situated within 50 meters of an ecological edge were more susceptible to predation than nests farther away. Nests in open areas rather than in tall vegetation were more likely to be destroyed by predators (Robinson and Bider 1988).

4.5 Rain conditions

The effect of rain on predation rate is unclear. Legler (1954) and Burger (1977) obtained a decrease of predation after heavy rain. Hammer (1969) speculated that because of heavy rainfall in 1967, nest detection by predators was inhibited decreasing the level of predation compared with previous years. However Wilhoft et al. (1979) and Bider (pers. comm.) observed an increase in predation after a heavy rain. Congdon et al. (1983) also observed an increase of predation during and shortly after rain on 6 day old nests. Unfortunately most authors gave no information on age of the nests and/or quantity of water (rain intensity and duration).

5 NEST CUES AND PREDATOR SENSES

Pyke (1978) stated that "in situations in which obtaining food is the most important factor, animals will prove to be moving either wholly or partly in response to sensory inputs in ways that maximize their foraging efficiencies". With reference to turtle nest predation, the factor "distance from water" reveals that depending on the predator involved, and thus its habitat use and movements, the impact on nests would differ. According to Snow (1982) and Semel and Nicolaus (1992), research should be oriented more toward this aspect of turtle nest predation. But it is impossible to record simultaneously the movements of numerous potential predators frequenting turtle nesting sites, limiting the suitability of this approach. The effect of the age of the nest and weather conditions on predation rate raise the importance of another component: sensory inputs which include nest characteristics that could be used by predators to locate nests. The sensory ecology of predators is poorly understood (Dusenbery 1992; Bernays and Wcislo 1994), particularly turtle nest predators (Wilhoft et al. 1979). Thus this project focuses on proximal turtle nest detection and the evaluation of the sensory perception of potential nest cues by two predator species, the raccoon and the striped skunk.

5.1 Nest cues

Different nest characteristics that could be used as cues by predators have been suggested in the literature.

5.1.1 Visual cues

5.1.1.1 Dark wet surface

It is reported that turtles sometimes urinate on the nest site before commencing to dig and sometimes urinate in the nest cavity while laying the eggs (Legler 1954; Mahmoud 1968; Patterson 1971; Ehrenfeld 1979). The dark wet soil, used to seal the nest after laying could contrast with lighter dry surrounding soil, constituting a visual cue.

5.1.1.2 Smooth surface

Some turtle species tamp the soil to cover their nests (Legler 1954; Mahmoud 1968; Auffenberg and Iverson 1979; Erhenfeld 1979; Linck et al. 1989) thus producing a smooth patch which could contrast with the surrounding rough ground. This ground surface difference could constitute a visual cue (Auffenberg and Iverson 1979).

5.1.2 Olfactory cues

5.1.2.1 Female turtle urine, cloacal mucus

The turtle's urine, as well as the cloacal mucus around the eggs, could be olfactory cues by which predators locate nests (Auffenberg and Iverson 1979; Stancyk et al. 1980). By contrast, Patterson (1971) found that urine of the desert tortoise (*Gopherus agassizi*) acted as a repellent to foxes and coyotes.

With time and following rain and growing vegetation, the visual and olfactory cues weaken and even vanish (Legler 1954; Congdon et al. 1983). This phenomenon could explain the high nest predation rate observed in the first 72 hours after laying and the reported decrease in predation over time (Petokas and Alexander 1980; Tinkle et al. 1981; Congdon et al. 1983, 1987; Christens and Bider 1987; Robinson and Bider 1988). The high nest predation observed after heavy rain could be due to a collapse of the nest-top creating a depression and even revealing the eggs (Bider, pers. comm.).

5.1.2.2 Metabolites and moisture from egg metabolism

Burger (1977) and Congdon et al. (1983) suggested that, during incubation, the metabolites produced by the embryos and released from the eggs could accumulate in the nest and constitute an olfactory cue detectable by predators. Also eggs that fail to develop and putrefy in the nest, could produce odors that attract predators (Congdon et al. 1983).

The moisture content around and in the nest could differ because digging brought up moister lower soil (Wilhoft et al. 1979; Linck et al. 1989), and also because of egg metabolism (Packard et al. 1985). This difference of soil moisture between the nest and the surrounding ground, and therefore difference of water evaporation and odor gradients, could be an olfactory cue (Wilhoft et al. 1979).

5.1.3 Tactile cues

5.1.3.1 Compaction

Wilhoft et al.'s (1979) experiment raised another interesting question. In their study, 83 false nests, some of them containing turtle eggs, dove eggs or ping-pong balls, were placed in a snapping turtle nesting area. The 34 ping-pong ball decoy nests were found by raccoons. Different measures were taken to avoid scent tracks and some nests were only found a few days after their installation. Wilhoft et al. (1979) suggested that perhaps the ground disturbance while digging the decoy nests produced olfactory cues. As raccoons were the predators involved in this study, another hypothesis could be proposed. Raccoons are known to use the sense of touch of their forepaws to locate food in water and on the ground (Whitney 1933; Tevis 1947; Ricard 1986; Sanderson 1987; McClearn 1992). The sensitivity of this sense in raccoons (Lyall-Watson 1963; Rensh and Dücker 1963; Welker et al. 1964) could help in detecting differences in soil compaction. Some female turtles tamp the soil to seal the nest and Patterson (1971) found that urine of the desert tortoise acted to harden the nest cover after laying. This difference of soil compaction and hardness between the nest and the surrounding ground could be a persistent tactile cue.

5.1.3.2 Moisture

The moisture of the nest surface could differ from surrounding ground because of female urine, the disturbance of the soil while digging (Wilhoft et al. 1979; Linck et al. 1989) or because of egg metabolism (Packard et al. 1985). This moisture contrast could constitute not only an olfactory cue but also a tactile cue, especially for raccoons.

5.1.4 Auditory cue

According to McMurtray (1986) and Bider (pers. comm.), the sound produced by hatchlings preparing to leave the nest could explain predation observed on nests just before emergence.

5.2 Predator senses

From the nest cues proposed, four senses could be involved in nest localization by the predators; sight, olfaction, touch and hearing.

5.2.1 Raccoon senses

The tactile sense is very well developed and widely used by raccoons searching for food. From neurophysiological studies by Welker and Seidenstein (1959), Zollman and Winkelmann (1962), Welker and Campos (1963), Welker et al. (1964), Turnbull and Rasmusson (1986) and behavioral studies by Whitney (1933), Tevis (1947), Rensh and Dücker (1963), Lyall-Watson (1963), Ricard (1986), Sanderson (1987), and McClearn (1992), touch has been recognised to be of primary importance. Their olfactory apparatus seems to be well developed and similar to that of the dog (*Canis familiaris*) and the marten (*Martes americana*), and more developed than that of the mink and the cat (*Felis domesticus*) (Ferron 1973). Raccoons seem to be color-blind (Michels et al. 1960; Jacobs and Deegan II 1992) but possess good visual acuity (Munn 1930; Fields 1936; Johnson and Michels 1958a,b; Hitchcock et al. 1963) and their vision is more similar to diurnally-adapted rather than nocturnally-adapted mammals (Jacobs and Deegan II 1992). According to Kaufmann (1982) they also should have excellent night vision because of a well-developed tapetum. The auditory threshold of detection and range of frequencies perceived have also been established for this species. They appear to have acuity similar to that of the cat (Wollack 1965) and were placed by Peterson et al. (1969) in the sensitivity group of the Asiatic black bear (*Selenarctos thibetanus*) and the tayra (*Eira barbara*). As no information is available about the intensity and frequencies of hatchling noise, it is impossible to know whether raccoons can effectively hear hatchling turtles.

5.2.2 Skunk senses

Information concerning skunks is scarce. This species is supposed to have weak vision (Verts 1967) and prefers auditory over visual stimuli to locate moving prey (Langley 1979). However, skunks appear to use olfaction while foraging (Langley 1979; Nams 1991) and would have a good sense of smell compared to vision (Carr 1974), as indicated by the well developed olfactory bulbs (Pilleri 1960).

III. OBJECTIVES

Since turtle nest localization by predators is not well understood, this project focused on possible nest cues used by the two principal predators of turtle nests in North America, the raccoon and the striped skunk. Also as this experiment is based on conditioning it provides an opportunity to compare learning abilities of raccoons, and adult and juvenile skunks using similar protocols.

The objectives of this project were:

a) to isolate potential turtle nest cues and create protocols to test them separately using a non-invasive technique.

b) to use subject behavioral responses to assess the potential value of these turtle nest cues. The leading principle of the protocol was based on the assumption that the more predominant the use of a sense by a given species, the faster the learning of a task (e.g. discrimination of a cue) involving this sense (Bitterman 1975; Kamil and Yoerg 1982; Jerison 1983).

c) to establish for each species a hierarchy among the cues tested. d) to make interspecific comparisons of turtle nest cue perception.

e) to make interspecific comparisons of learning abilities.

f) to compare juvenile to adult skunks to determine possible inter-age class difference in sensory perception and learning rate, and infer the role of learning in the individual development of turtle nest localization.

My hypotheses (H.) and predictions are:

H_1. The tactile sense is predominant in raccoons when compared to vision.

Therefore I expect that raccoons will learn tactile cue discrimination faster than visual cue discrimination.

As no information is available on olfaction relative to the other senses in raccoons, it is difficult to propose any hypothesis and prediction about performances in the olfactory test relative to the visual and tactile tests. Therefore comparisons of this sense with vision and touch senses are exploratory.

H_2. The olfactory sense is predominant in skunks when compared to vision and touch. Therefore I expect that skunks will learn the olfactory cue discrimination more quickly than the other cue discriminations.
It is difficult to propose predictions about sight relative to touch in skunks with the available information about these senses.
Here again comparisons between tactile and visual tests are mostly exploratory.

At the interspecific comparison level, I expect that (assuming that the species-specific rate of learning does not differ between raccoons and skunks), tactile discrimination will be learned faster by raccoons than by skunks.

More information is available on the sight of raccoons than on the sight of skunks. Raccoons seem to possess sight similar to diurnally-adapted mammals whereas skunk vision is thought to be weak. As these species are being compared for the first time using the same protocol (and under red light simulating night conditions), no prediction is proposed on the outcome of this interspecific comparison. Both species seem to possess a good olfaction but as they are being compared for the first time in a same experiment, the outcome of this interspecific comparison is unpredictable.

Learning abilities may differ between raccoons and skunks. However since this is the first experiment to compare raccoons and skunks with the same protocols, no particular predictions are proposed on the outcome of the interspecific comparisons.

Concerning juvenile skunks, lack of knowledge on the development of sensory capabilities limits predictions. Nonetheless as for the adult skunk, I expect that juvenile skunks will learn the olfactory cue discrimination faster than the other cue discriminations.

For juvenile and adult skunk comparisons, again the lack of information on the neurophysiological development of skunks precludes the proposal of predictions. Not knowing the learning abilities of the juvenile subjects at the time they are used in the tests, and having limited experience due to their conditions of captivity, comparisons are more of an exploratory character.

IV. MATERIAL AND METHODS

1 SUBJECTS

1.1 Origin

Wild raccoons and striped skunks were captured in spring (April to July) 1991 and 1992 using Havahart (0.30x0.30x0.90 m) and Tomahawk (0.30x0.30x0.90 m) live-traps. These live-traps were baited with peanut butter and sardines. Twelve raccoons and 14 skunks were captured; Seven raccoons and 11 skunks in and around the St.Lawrence Valley Natural History Society Ecomuseum at Ste-Anne-de-Bellevue, Québec; Two raccoons and one skunk at Monk Point, Ile Bizard, Québec; Two skunks in Pincourt, Québec, and three raccoons in Hudson, Québec. The skunks caught in spring 1992 were kept over winter at the Ecomuseum grouped in cages provided with special insulated boxes. In spring 1993, two females gave birth to four young and five young respectively. Three newborn of each litter survived and were kept with their mother for 75 days, before being transferred to individual cages.

1.2 Selection

All animals were weighed and sexed. The age class was determined using anatomical criteria and weight (Verts 1967; Mech et al. 1968; Sonenshine and Winslow 1972; Sanderson 1987; Traversy et al. 1989), tooth wear (Grau et al. 1970) and general condition. As this method is not precise, three age classes were used: <1 year, juveniles; <2 years, "yearlings", some of which could have been older; ≥2 years, adults. Although a homogeneous sample of a single age and sex would have been preferred this was impossible. Lists of raccoons, skunks and juvenile skunks used in the experiments are presented in Tables 4.1, 4.2 and 4.3.

1.3 Housing

The animals were housed in individual outdoor cages. Wire mesh (6x3 cm) was used in the raccoon cages (2x1.2x1.8 m) which were set on a concrete floor. A roof covered half of the cage. Each cage contained a wooden shelter (0.3x0.5x0.3 m), 30 cm above ground, equipped

Table 4.1. Identification number, sex (male M or female F), presumed age (in years), date of capture, site of capture and weight (in Kg) of the raccoons used in 1991 and 1992 experiments.

	SUBJECT #	SEX M or F	AGE (in years)	DATE OF CAPTURE	SITE OF CAPTURE	WEIGHT (in Kg)
1991	R1	F	<2	08/06	Ste-Anne	5.5
	R2	M	<2	12/06	Ste-Anne	5.5
	R3	F	<2	12/06	Ste-Anne	6.5
	R4	M	<2	18/06	Ste-Anne	7-7.5
	R5	M	<2	20/06	Ste-Anne	6.0
	R6	F	<2	26/06	Ste-Anne	6.0
1992	R7	F	<2	21/05	Ste-Anne	5.0
	R8	M	≥2	18/06	Hudson	7.0
	R9	M	<2	18/06	Monk Pt	6.5
	R10	F	<2	19/06	Monk Pt	4.5
	R11	F	<2	19/06	Hudson	4.0
	R12	M	≥2	19/06	Hudson	7.0

Table 4.2. Identification number, sex (male M or female F), presumed age (in years), date of capture, site of capture, and weight (in Kg) of the skunks used in 1991, 1992 and 1993 experiments.

	SUBJECT #	SEX M or F	AGE (in years)	DATE OF CAPTURE	SITE OF CAPTURE	WEIGHT (in Kg)
1991	S1	M	<2	06/06	Ste-Anne	1.5
	S2	M	≥2	08/06	Kirkland	3.5
	S3	M	<2	20/06	Ste-Anne	2.0
	S4	F	<2	02/07	Ste-Anne	2.0
	S5	M	≥2	16/07	Ste-Anne	2.5
1992	S6	M	<2	29/04	Ste-Anne	2.5
	S7	M	≥2	01/06	Pincourt	6.0
	S8	M	≥2	01/06	Ste-Anne	3.5
	S9	M	<2	16/06	Monk Pt	2.0
	S10	M	<2	30/06	Ste-Anne	2.5
	S11	F	<2	18/07	Ste-Anne	1.5-2.0
	S12	F	<2	20/07	Pincourt	2.5
	S13	F	<2	22/07	Pincourt	1.5
1993	S14	M	≥2	01/04	Ste-Anne	3.0

Table 4.3. Identification number, sex (male M or female F), birth date, date of separation from mother, and date of isolation in an individual pen of the juvenile skunks used in the 1993 experiments.

SUBJECT #	SEX M or F	BIRTH DATE	SEPARATION DATE	ISOLATION DATE
LI	F	03/05	25/07	02/08
LII	M	03/05	25/07	02/08
LIII	M	03/05	25/07	02/08
PI	M	16/05	02/08	15/08
PII	F	16/05	02/08	15/08
PIII	F	16/05	02/08	15/08

with a horizontal sliding door that could be closed from outside the cage. This box was also used to transport the animal.

Skunks were housed in two blocks of four individual pens 1.8x1.2x1.8 m each. Walls were made of wire mesh (6x3 cm). Block 1 was set on a floor consisting of sand over concrete. Block 2 was set on a floor consisting of soil over metallic screen mesh (4x4 cm). Each pen contained a wooden box (0.27x0.3x0.3 m) equipped with a vertical sliding door that could be closed from outside the cage. The cages were completely covered with a roof.

1.4 Feeding

The food intake was controlled to maintain constant weight throughout the experiment. The daily ration was determined for each animal and adjusted depending on the animal's response to food rewards during the tests. They were fed soon after they performed in a session. The total ration was generally eaten in the hour following the presentation, thus the animals fasted for approximately 20 hours before the following session. The raccoons received Banner-Bit (small bit) dog food pellets, sometimes supplemented with fruit. The food pellets were also used as rewards in the experiments. The skunks were fed with a mix of 1/4 Science diet-Adult cat pellets and 3/4 Purina Cat Chow, sometimes supplemented with fruit. Because it appeared to be their favorite food, Science-diet pellets were used as rewards in the tests.

Since the experiments lasted into late fall, food intake was increased progressively in October so that the animals accumulated fat to overwinter. This increase in their food intake did not seem to affect their response to the reward in the tests. They were fed ad libitum between the end of the experiments and their release. Water was given ad libitum at all times.

1.5 Health care

All the animals were vaccinated for rabies and distemper. Some of them were also treated for intestinal worms. The musk glands of skunks were not removed so that the animals were releasable after the experiments.

2 APPARATUS

2.1 Test arena

In 1991 and 1992, the test arena was placed in a room within a barn on Macdonald Campus of McGill University. In 1993, the arena was moved to the St. Lawrence Valley Natural History society Ecomuseum on the Macdonald campus. It consisted of a wooden chamber (Fig. 4.1) set on a concrete floor covered with 15 cm of dry sand. A sliding door (c) allowed the subject to move between the rest-box (d) and the arena (e). Access to the arena was through a lateral door (f). The animals could be seen through a one-way window (g) situated over the sliding door. I was able to see the animal enter and exit the arena through a mirror (h) placed on the opposite wall. During the experiments, the arena was illuminated with a red light (60 watts) situated in the middle of the chamber. The room and the rest-box were in almost complete darkness. Five receptacles (i), plastic containers 10 cm in top diameter, and 10 cm deep were placed in the sand so that the tops were at ground level. Each receptacle was 1.20 m from the animal entrance and separated from its neighbor by 30 cm.

2.2 Cue-pots

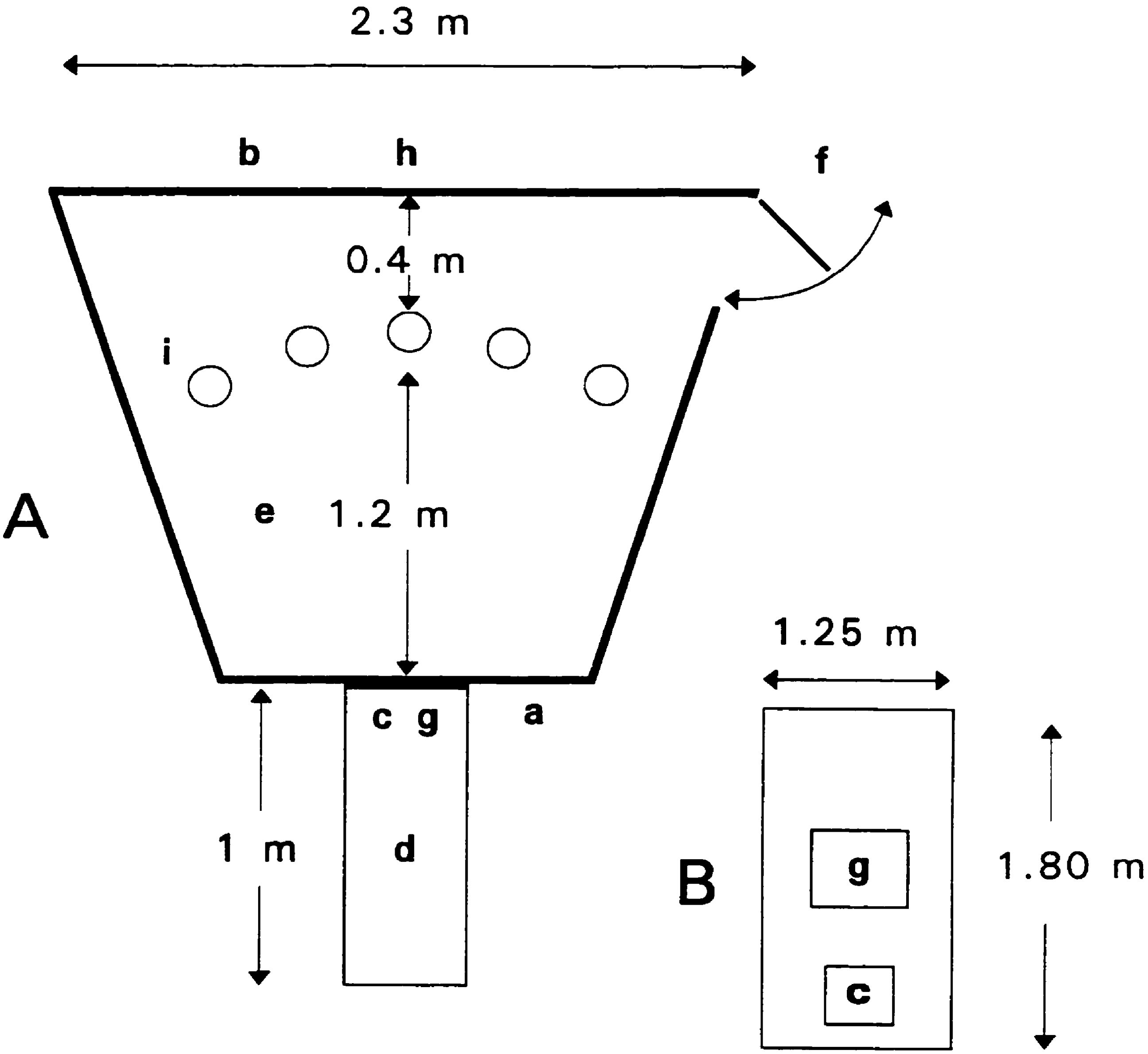
Plastic cue-pots identical to the receptacles described above were filled appropriately for the cue tested and set in the five receptacles. To avoid position preferences by the subjects, observed after a certain period of training in some studies that used two-choice discrimination (Shell and Riopelle 1957; Doty et al. 1967), five pots rather than two pots were used in each experiment. In addition, to choose one cue-pot among five pots instead of one out of two reduced the probability that the subjects performed a correct response by chance (Fellows 1967).

2.2.1 Visual cues

Two different potential visual cues were tested.

. dark surface - in this test the cue-pot was filled with wet dark sand while the other pots were filled with dry light sand. To avoid the use of other senses such as touch or olfaction, all the pots were sealed with a glued transparent hard plastic disk (4 mm thick).

Figure 4.1. Experimental arena used for the behavioral tests, located in a room within a barn on Macdonald Campus in 1991 and 1992, and at the Ecomuseum in 1993.



Legend

A- Plan View; a. Front, b. Back, c. Sliding door, d. Rest-box, e. Arena, f. Lateral door; g. One-way window; h. Mirror; i. Receptacles

B- Upright View of front (a); g. One-way window, c. Sliding door entrance to rest-box.

. surface texture - in 1991, the pots were filled with dry sand, substrate sometimes used by female turtles for nesting (Ehrenfeld 1979; pers. obs.). The surface of the cue pot was smoothed while the surface of the other pots were roughened. The pots were not sealed and it was ensured that the animals did not use touch to find the cue pot. In 1992 and 1993, the cue pot was filled with wet fine compacted clay, substrate used sometimes by female turtles for nesting (Legler 1954; Ehrenfeld 1979; pers. obs.) and dried slowly to avoid formation of cracks on the surface. It resulted in a hard smooth surface. The other pots contained clay in granules (diam. 4 mm to 22 mm). In 1992 and 1993, but not in 1991, all pots in all trials were sealed with a transparent plastic disk.

2.2.2 Olfaction cue

All the pots were filled to the top with dry sand. The cue pot received 0.2 ml of turtle urine delivered with a micropipet to the surface centre. The other pots received 0.2 ml of distilled water.

Turtle urine collection

Female painted turtles were captured in the Ecomuseum turtle pond in June and July 1990, 1991 and 1992. Soon after capture the turtles were placed in a urine collector. It consisted of a plastic basin 0.30x0.24x0.15 m sloping 25° to 30° on a wooden frame. In the lowest corner a hole one cm in diameter was covered with a plastic screen (1x1 mm mesh) to filter large particles of excrement. The urine then ran down a plastic tube housing a paper filter laid on a second plastic screen (1x1 mm mesh). This retained the small particles. At the end this tube was connected to a sterile conical tube (Falcon 50 ml) which received the urine. The turtles generally urinated within one or two hours after being captured. The urine sample was placed in a freezer. The basin and filtering tube were washed with 75% alcohol and rinsed with distilled water before being reused.

2.2.3 Touch cue

The cue pot contained hard dry clay covered with a thin (2 to 3 mm) layer of dry loose fine clay. The other pots contained only loose dry fine clay. All the pots therefore appeared identical to the subject through sight and olfaction, and discrimination was only possible by touch.

3 EXPERIMENTAL PROTOCOL

3.1 Habituation

Before the conditioning trials began, the wild animals had to be accustomed to their captive conditions, and to me. Every day, I enclosed the subjects in their box while cleaning their cages. This got them used to being enclosed in their box for transport. After cleaning, I released them from their box, fed them and stayed near the cages for one to two hours. This procedure had two goals. First, it familiarized the animals to my presence, which was particularly necessary for the skunks which were shyer than the raccoons. As the skunks were not "descented" I also had to be more cautious with them and to take more time to acclimate them to my presence. Second, this schedule forced the animals to be active during the day when the experiments were to take place.

3.2 General experimental design

The experiments consisted of choice-tests based on food conditioning with a variable reward reinforcement. In order to establish this conditioning the subjects were trained in a daily session. The experimental design included two successive stages:

- a training period, or Pre-test, to habituate the animals to the experimental apparatus and routine, and to establish the food-conditioning.
- a test-period which started when the subject had successfully completed the Pre-test. It included all the different nest-cue discrimination tests.

3.2.1 Session general procedure

In 1991 the skunks worked in the morning and raccoons in the afternoon. In 1992 the schedule was reversed. In 1993 juvenile skunks worked in the morning and the other skunks worked in the afternoon. The daily schedule (subject order) was randomly determined in order to vary the training time of each subject from day to day. Each session consisted of five successive trials, separated by a four minute interval, which gave sufficient time to prepare the arena for the next trial.

3.2.1.1 Preparation of sessions

The designated subject was transported in its box to the test arena. In the test-room, the subject was transferred from the transport-box to the rest-box enticing it with food pellets. Those which were sometimes reluctant to move, even after one or a few days of food restriction or deprivation, were sprayed with water through a hole in the box. This harmless technique was efficient and generally proved unnecessary after a few days of training. Date, time, room temperature and relative humidity were recorded on the subjects record-sheet.

The five pots were placed in the arena. The position of the cue-pot was randomly assigned by lottery but differed between successive trials. Before leaving the arena, I erased my footprints in the sand with a broom.

3.2.1.2 Trial procedure

The room light was turned off and the guillotine door was opened allowing the animal to enter the arena. A stopwatch was started as the door opened. As the animal entered the arena, the guillotine door was lowered gently, and the time again recorded. This time data was used to evaluate the "motivation" of the subject and thus adapt the procedure in the next trial or session. I recorded a simple behavioral repertoire. Roman numerals were attributed to the arena corners, and pots were numbered from one to five, both starting at the left of the observation point.

As the subject approached the cue-pot, depending on the test, the subject either looked at the cue-stimulus, and smelt it or touched it. Each time the subject visited the cue-pot the door to the rest-box was opened and the animal was rewarded with food when inside. Four different behavioral scenarios determined the size of the reward:

a. If after visiting the cue-pot the subject visited other pots before coming back to the box to get the reward, it received only one food pellet.

b. If the animal came back directly to the box after visiting the cue-pot but after the door was opened, it received three food-pellets given one at a time.

As the training progressed, the response b was performed more often as the association between cue-pot and food-reward was acquired by the subject. At this point, I increased the delay between the finding of the cue-pot and the opening of the door. Two other responses were possibly performed:

c. If the subject reacted to the cue-stimulus and returned directly to the box before the door was opened, it received six food-pellets.

d. The subject sometimes reacted to the cue-stimulus and waited looking, smelling or touching the cue-pot while glancing at the door. If it continued this action until the door opened, at which time it returned to the box, it received six food-pellets.

These latter two responses were considered correct in that the subject indicated a choice or selection of one pot by its behavior. Six food pellets at a time was the highest reward given. Training was continued until the subject attained at least four correct responses in a session of five successive trials, i.e. a success rate of 80% in a session. The total number of trials performed by the subject in a test (including the last five trials) was the performance to achieve 80% success rate in a test. This value was the unit of measurement of success for an individual and was used in the statistical analyses. The cue discrimination was then considered learned and the subject was presented with a new test.

3.2.2 Pre-test

Pre-test in 1991 consisted of offering four empty pots and one cue-pot containing a food pellet as a cue-stimulus. In 1992 and 1993 I replaced the food-pellet with a white ping-pong ball. I chose this stimulus because it looked like an egg and might elicit a particular reaction of the subjects. Moreover it was a stimulant to all the senses I was testing (i.e. sight, touch and olfaction). When the animal found, looked at, smelt, touched and even bit the ball, I opened the guillotine door to give it access to a reward according to the variable reward reinforcement schedule described in section (3.2.1.2 Trial procedure).

3.2.3 Cue-tests

3.2.3.1 Experimental design

Each subject had to perform up to four different cue-tests after it completed the Pre-test.
Adults.- The discrimination tests were presented in the following order: First, Contrast-test (visual contrast of dark vs. light sand); Second, Texture-test (visual texture smooth vs. rough surface); Third, Olfaction-test (turtle urine vs. distilled water); and fourth, tactile Compaction-test (compacted vs. loose clay). In 1991 raccoons performed in the first three cue-tests with sand substrate in the Texture-test. In 1992, a new group of raccoons performed the tests in the same order but the texture was smooth vs. granular clay surface, and the Compaction-test was added. In 1991, the skunks (S1, S2, S3, S4, and S5) did not succeed in the Pre-test before their release in the fall. In 1992, a new group of six skunks (S8, S9, S10, S11, S12 and S13) performed the Pre-test and then, except for S9, the Contrast-test. Subject S8 also performed in the Olfaction-test. In 1993 skunks S10, S11, S12, S13 were submitted for the second time to the Pre-test and the Contrast-test. They were then presented for the first time with the other cue-tests in the order: Texture-test (smooth vs. granular clay surface), Olfaction-test and Compaction-test. Subject S14 performed in the Pre-test, the Contrast-test and the Olfaction-test.

Juveniles.- In 1993, striped skunks of the year were separated randomly into two samples, lot 1 and lot 2. The lots were given tests in different orders. Lot 1 with the animals L1, L3 and P3, were tested in the following order: Compaction-test, Olfaction-test, Contrast-test and Texture-test (smooth vs. rough clay surface). Lot 2 with the animals L2, P1 and P2, were tested in the following order: Contrast-test, Olfaction-test, Compaction-test and Texture-test (smooth vs. rough clay surface). These schedules were used in order to analyze the possible influence of the test's order on the subjects'performances. The Texture-test was run last because of the possibility, based on the data obtained with adults, of not having enough time to run all the tests before winter.

3.2.3.2 Cue-test procedure

The general procedure described in section (3.2.1.b. Trial procedure) was the same for all the tests. However, the preparation of the arena for a trial, i.e. the set-up of the pots, differed according to the cue-test.

Vision.- All the pots were sealed with a transparent plexiglas disc so the animals could only use sight to discriminate between the pots. To increase the reliability of the test, by preventing the use of other cues e.g. odors, all the plastic tops were cleaned with 75% alcohol between each trial. With this cleaning, any possible olfactory cues the animal could have left by touching or urinating on the pot were removed. In the 1991 Texture-test with raccoon, the pots were not sealed with a plastic disc to allow the preparation of the sand surface. All the pots were changed between each trial and special attention was given to record the possible use by the subjects of touch to discriminate between the pots, which they did not use.

Olfaction.- In this test the five pots were filled with dry sand. The cue pot received 0.2 ml of turtle urine solution delivered with a micropipet. This drop of urine was deposited at the centre surface of the pot one minute before the beginning of the trial. Then the four other pots received each 0.2 ml of distilled water at the surface centre, so that all pots were visually similar. All pots were changed between each trial taken from a reserve of 50 pots filled with clean sand.

Touch.- The cue pot as well as the other pots touched by the subject were changed between each trial. As the session progressed all the pots were finally changed at least once (taken from a reserve of 25 pots and from a reserve of 10 cue-pots). This avoided any possible use of smell by the subject to discriminate between the pots from one trial to the next.

4 STATISTICAL ANALYSES

In order to use as much data as possible, samples as large as possible, according to the tests performed by the subjects, were used in the different statistical tests and comparisons. In 1991 the raccoon sample consisted of subjects R1, R2, R3, R4, R5 and R6 (n=6). As subject R1 escaped from its enclosure after performing the Pre-test, the sample size was reduced to n=5 (subjects R2, R3, R4, R5 and R6). In 1992 the raccoon sample consisted of subjects R7, R8, R9, R10, R11 and R12 (n=6). Subjects R11 and later R12 developed erratic behavior during the tests (walking back and forth along one wall, stopping on each pot and indicating no choice, refusing to leave the rest-box). As no progress was observed (and the 80% success rate not achieved), the subjects were removed from the experiments. Therefore the raccoon sample consisted of subjects R7, R8, R9, R10 and R12 (n=5) in part of the analysis. Subjects R7, R8, R9 and R10 (n=4) were the only one to perform all the cue-tests.

Due to repeated training by some adult skunks in the Pre-test and the Contrast-test, four different samples were composed; SI with subjects S10, S11, S12, S13 (n=4); SII with subjects S8 and S14 (n=2); SIII with subjects S8, S10, S11, S12, S13 and S14 (n=6) and SIV with subjects S8, S9, S10, S11, S12, S13 and S14 (n=7). For the juvenile skunks lot 1 with subjects L1, L2 and P3 (n=3) and lot 2 with subjects P1, P2 and L3 (n=3) were sometimes pooled (n=6).

Non-parametric statistics were used because of small sample size ($n \leq 6$ in most comparisons) and the impossibility of meeting assumptions of parametric statistics (data distribution unknown).

Cue discriminations

The results are expressed in total number of trials (x_{ik}) performed by the subject i to obtain an 80% success rate in a test k (individual performance). For intraspecific male-female comparisons, a Mann-Whitney *U*-test (referred to as Mann-Whitney *U*) was used (Daniel 1990).

For species-specific multi-comparisons of the different cue-test performances, Friedman two-way analysis of variance (referred to as Friedman two-way-ANOVA) was used followed by multiple comparisons procedure (equivalent to Fisher's least significant difference method) when possible (Conover 1980).

For interspecific comparisons, performance ratios were used in order to limit individual and species-specific effects of learning rate on performances. A performance ratio represents, for an individual i, a proportion of learning effort necessary to achieve the desired success rate (80%) in a particular test, or number of trials in a test k (x_{ik}), divided by the total number of trials required for learning all k tasks at the same success rate (Σx_{ik}).

$$\text{ratio } x_{ik} = x_{ik} / \Sigma x_{ik}$$

with a maximum of k=4 cue-tests considered (Pre-test excluded).

Learning

In order to evaluate the species-specific and the age effects on learning performances, performances (number of trials to achieve 80% success rate) instead of performance ratios were compared between raccoons and skunks, and between adult and juvenile skunks. For these comparisons, a Mann-Whitney *U*-test (referred to as Mann-Whitney *U*) was used (Daniel 1990).

As the same animals were used in successive tests, the possible inter-problem transfer of learning sets (Riopelle 1953) was assessed through correlation between performances in the Pre-test and the Contrast-test (two successive tests) and by comparing relative variability (Lewontin 1966) between tests. In order to compare between raccoon and skunk, data were first analyzed at intra-species level.

The relation between successive performances in the Pre-test and the Contrast-test for raccoon and skunk, and the Pre-test and the Contrast-test in 1992 and 1993 for skunk were assessed by computing the Spearman (r_s) rank correlation coefficient (Daniel 1990). It was associated with species-specific comparisons between performances in the Pre-test and the Contrast-test using Wilcoxon matched-pairs signed-ranks test (referred to as Wilcoxon signed-ranks test) (Siegel and Castellan 1988; Daniel 1990). This statistical test was also used to compare performances between the Pre-test and the Contrast-test performed twice (first in 1992 and again in 1993) by some skunks.

The squared ranks test for variances (Conover 1980) was used to compare variances between similar test performances of 1991 and 1992 raccoons, and lot 1 and lot 2 juvenile skunks. It was done in order to detect a possible effect of the protocol on the performance variability, the protocol differing in the Pre-test and the Texture-test for raccoons, and the test order of presentation for juvenile skunks. The relative variability of test performances was compared at the intraspecific level (raccoon 1991 and 1992, adult skunks), at interspecific and at inter-age level (adult-juvenile skunks). The measure of relative variability is generally expressed as the coefficient of variation (CV, sample standard deviation divided by the sample mean). It allows variability comparison especially in case of unequal sample means. In order to use the non-parametric statistical test, the variance of the logarithms of the performances ($S^2 \ln x$) was used instead of the coefficient of variation. The comparison of these variances is equivalent to a comparison of the coefficients of variation (Lewontin 1966). These variances were compared using the squared ranks test for variances for two variances or several variances (Conover 1980). Though not directly compared, coefficients of variation are given in percentage (CVx100) as they are easier to understand than the equivalent logarithms of a variance.

As comparisons are sometimes multiple and due to a lack of information on senses or learning abilities, in all the statistical tests the null hypothesis was that there is no significant difference (inter-sample, inter-sex, inter-test, inter-age, interspecific) between the test performances or test performance ratios. Therefore the statistical tests were two-tailed tests. Statistical tests were considered significant at an associated probability (P) lower than a level of significance $\alpha = 0.05$. In Wilcoxon matched- pairs signed-ranks test in the case of skunks data, because of small sample size ($n=4$), the lowest possible limit of the probability was 0.068 (Siegel and Castellan 1988). When exact probability associated with the test statistic was not available, the closest minimum probability ($P_{Tab.}$) obtained from a statistical table (Conover 1980; Siegel and Castellan 1988) was indicated as ($P > P_{Tab.}$) or ($P < P_{Tab.}$). Computation of descriptive statistics and part of the statistical analysis, were executed with Lotus 1-2-3 (Version 3.1) (Lotus Development Corporation 1983, 1989) and Systat (Wilkinson 1989).

CHAPTER V - ADULT RACCOONS

1 INTRODUCTION

Trials with raccoons were carried out in 1991 and 1992. Since some modifications were added to the Pre-test and the Texture-test protocols in 1992 (see Material and Methods), the data were treated separately and then compared. The animals used are listed in Table 4.1. Individual performances (number of trials to achieve 80% success rate) in the Pre-test and the cue-tests are given in Appendix 1 for both years.

2 RESULTS

2.1 1991 results

In 1991, six raccoons, three males and three females, were trained. No significant differences were found between male and female performances in the Pre-test (Mann-Whitney *U*, $P=0.83$, $n_♂=n_♀=3$), in the Contrast-test ($P=0.56$, $n_♂=n_♀=3$), the Texture-test ($P=0.56$, $n_♂=3$, $n_♀=2$) or the Olfaction-test ($P=0.20$, $n_♂=3$, $n_♀=2$). Therefore male and female data were pooled for the remaining analyses (Table 5.1, Fig. 5.1).

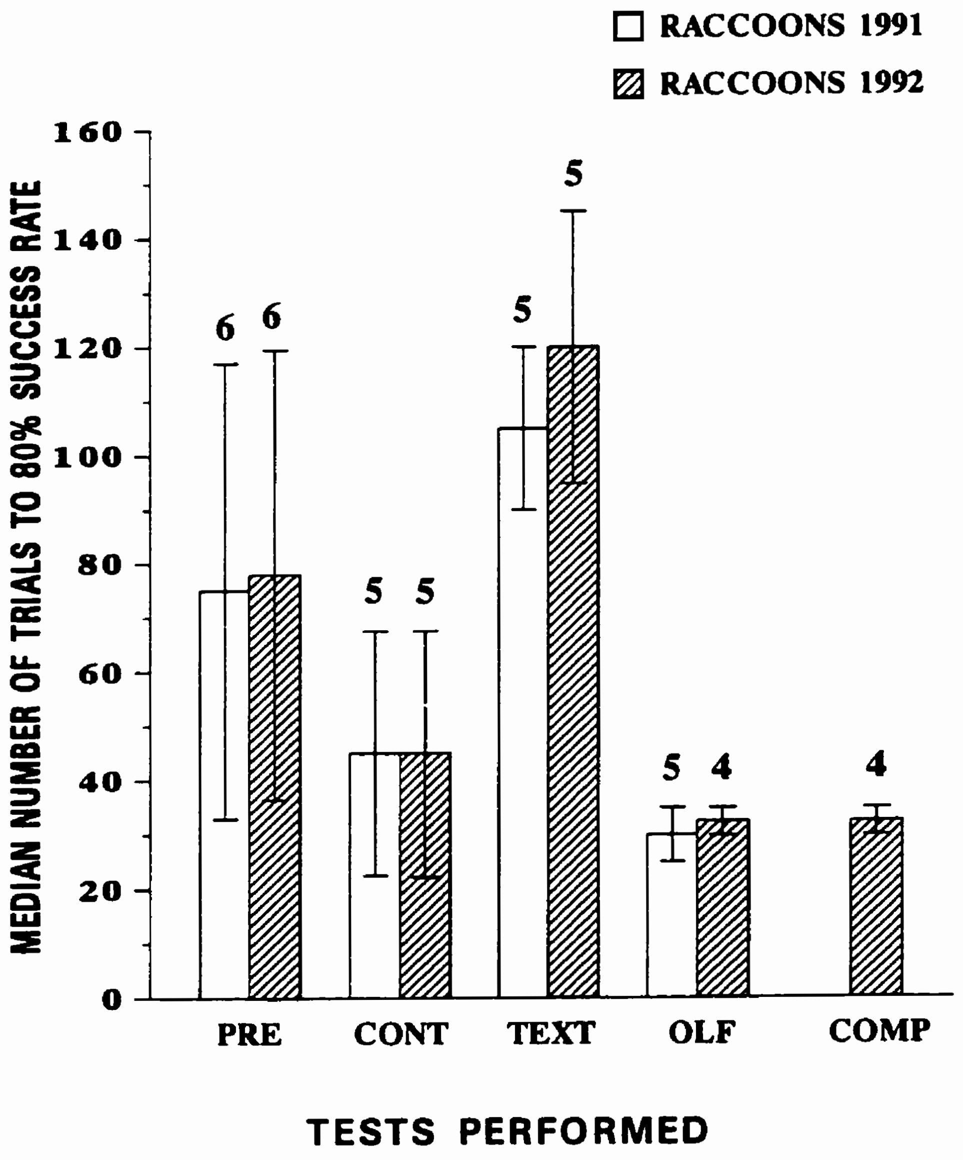
2.1.1 Pre-test and Contrast-test 1991

There was no significant difference between performances in the Pre-test and the Contrast-test (Wilcoxon signed-ranks test, $P=0.22$). In fact individuals R6 and R2 performed more trials in the Contrast-test than in the Pre-test and the reverse was true for subjects R3, R4 and R5 (Appendix 1). Also the disparity in the number of trials of individual performances in these two tests varied from one individual to another and was associated with high inter-individual variability as revealed by relatively high coefficients of variation in both tests ($CV_{PRE}=36.1\%$ and $CV_{CONT}=37.6\%$). There was no significant difference between variances of the Pre-test and the Contrast-test (Squared ranks test for variances, $P>0.60$). Also no significant correlation

Table 5.1. Mean performance (number of trials) to 80% success rate (MEAN) and dispersion statistics of raccoons 1991 in the different tests: Pre-test (PRE); Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF). Sample size (n), standard deviation (SD), standard error (SE), and coefficient of variation (CV=SD/MEAN, expressed in %).

TEST	n	MEAN	SD	SE	CV
PRE	6	84.7	30.5	12.5	36.1
CONT	5	52.0	19.6	8.7	37.6
TEXT	5	106.0	11.9	5.3	11.3
OLF	5	30.0	3.5	1.6	11.8

Figure 5.1. Raccoon median performances (number of trials) to 80% success rate in 1991 and 1992 in the Pre-test (PRE) and the cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). Vertical lines give range. The number above each bar is the sample size.


☐ RACCOONS 1991
▨ RACCOONS 1992
MEDIAN NUMBER OF TRIALS TO 80% SUCCESS RATE
0
20
40
60
80
100
120
140
160
6
6
5
5
5
5
5
4
4
PRE
CONT
TEXT
OLF
COMP
TESTS PERFORMED

appeared between performances in the Pre-test and the Contrast-test (r_s=-0.8, P>0.10, n=5). These intra and inter-individual differences of the learning rates explained the absence of significant correlation. I interpret this to mean a relative independence between the Pre-test and the Contrast-test success.

2.1.2 Inter cue-test comparisons

2.1.2.1 Analysis of variance by ranks

A Friedman two-way ANOVA comparing success in the Contrast-test, the Texture-test and the Olfaction-test indicated significant differences (T_2=91, P<0.01, n=5). A multiple comparison test indicated that the best performances (e.g. smallest number of trials to 80% success) were obtained in the Olfaction-test, the worst performances (e.g. largest number of trials to 80% success) in the Texture-test, with intermediate performances in the Contrast-test (α=0.05, | Rj-Ri | >1.63, df=8; Olfaction/Contrast, P<0.0005; Olfaction/Texture, P<0.0005; Contrast/Texture P<0.0005).

2.1.2.2 Relative variability

The coefficient of variation tended to decrease during the experiment from CV=37.6% (n=6) in the Contrast-test to CV=11.8% (n=5) in the last Olfaction-test (Table 5.1). The comparison of variances of performance logarithms indicated that at least one variance was different (Squared ranks test for several variances, T_2=7.82, P<0.03, df=3). The cue-tests were compared two by two. There was no significant difference between relative variability of the Texture-test (CV=11.3%) and the Olfaction-test (CV=11.8%) (P>0.80). There was a decrease between the Contrast-test (CV=37.6%) and the Texture-test (CV=11.3%) coefficient of variation with a significant difference in relative variability (P<0.01). There was also a significant difference of relative variability between the Contrast-test and the Olfaction-test (P<0.02).

2.2 1992 results

2.2.1 Reaction to ping-pong ball

In 1992, a ping-pong ball was used as conditioning stimulus in the Pre-test. The behavior of the subjects toward this stimulus is presented in Table 5.2. All the individuals touched the ball

Table 5.2. Raccoon behavior toward the ping-pong ball stimulus in the 1992 Pre-test, indicating the trial number (day number in brackets) when for the first time the subject: Smelled (nose close to or on the ball), touched with one or two forepaws, or bit the ball.

SUBJECT	SMELL	TOUCH	BITE
R7	1 (1)	1 (1)	10 (5)
R8	12 (4)	11 (4)	-
R9	3 (3)	4 (3)	4 (3)
R10	2 (1)	4 (3)	4 (3)
R11	6 (4)	6 (4)	10 (5)
R12	2 (1)	5 (4)	5 (4)

during the third or fourth day of the Pre-test, subject R7 even touching the ball in the first trial and biting it nine trials later (in the fifth day of testing). The first touch was associated with biting for individuals R9, R10 and R12, whereas for R11 biting occurred in the tenth trial in the fifth day of testing. Subject R8 never bit the ball. The delay in touching and especially biting the ball suggests that the ball was not a good egg-lure or that the subjects had no previous experience with eggs.

2.2.2 Sex differences

In 1992, six raccoons, three males and three females, were used. No significant differences appeared between male and female performances in the Pre-test (Mann-Whitney *U*, $P=0.51$, $n_{♂}=n_{♀}=3$) or the Contrast-test (Mann-Whitney *U*, $P= >0.08$, $n_{♂}=3$, $n_{♀}=2$). In the Olfaction-test and the Compaction-test, the female sample size ($n=1$) was too small to run a statistical test. However performances of males and this female were in the same range (Appendix 1). Therefore male and female data were pooled for the remaining analyses (Table 5.3, Fig. 5.1).

2.2.3 Pre-test and Contrast-test 1992

There was no significant difference between performances in the Pre-test and the Contrast-test (Wilcoxon signed-ranks test, $P=0.08$). Also the disparity on the number of trials in individual performances of these two tests varied a lot from one individual to another and was associated with high inter-individual variability as revealed by relatively high coefficients of variation in both the Pre-test ($CV=36.4\%$) and the Contrast-test ($CV=40.2\%$) (Table 5.3). There was no significant difference between the variances of the Pre-test and the Contrast-test (Squared ranks test for variances, $P>0.50$). Also there was no significant correlation between performances of these two tests ($r_s=0.075$, $P>0.50$, $n=5$). These intra and inter-individual differences of the learning rates explained the absence of significant correlation between success in the Pre-test and the Contrast-test.

2.2.4 Inter cue-test comparisons

2.2.4.1 Analysis of variance by ranks

In 1992, the subjects performed an additional compaction cue-test. When integrating these data

Table 5.3. Mean performance (number of trials) to 80% success rate (MEAN) and dispersion statistics of raccoons 1992 in the different tests: Pre-test (PRE); Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). Sample size (n), standard deviation (SD), standard error (SE), and coefficient of variation (CV=SD/MEAN, expressed in %).

TEST	n	MEAN	SD	SE	CV
PRE	6	81.7	29.7	12.1	36.4
CONT	5	47.0	18.9	8.4	40.2
TEXT	5	117.0	22.8	10.2	19.5
OLF	4	32.5	2.9	1.4	8.9
COMP	4	31.2	2.5	1.2	8.0

in the ANOVA, it indicated significant differences ($T_2=5.83$, $P<0.025$). A multiple comparison test ($\alpha=0.05$, $|Rj-Ri|>5.48$, df=9) resulted in the following differences: Contrast/ Texture ($P<0.05$), Olfaction/ Texture ($P<0.01$), Compaction/ Texture ($P<0.005$). The other comparisons were not significantly different: Contrast/Olfaction ($P>0.20$), Contrast/Compaction ($P>0.20$) and Olfaction/Compaction ($P>0.80$).

To summarize, similar good performances were obtained in the Olfaction-test and the Compaction-test and the worst performances in the Texture-test. Performances in the Contrast-test are similar to performances in the Olfaction-test and the Compaction-test for subjects R8 and R10 but poorer for subjects R7 and R9.

2.2.4.2 Relative variability

The coefficient of variation decreased during the experiment from CV=40.2% (n=5) in the Contrast-test to CV=8.0% (n=4) in the last Compaction-test (Table 5.3). The comparison of performance logarithms indicated no significant difference (Squared ranks test for several variances, $T_2=6.75$, $0.05<P<0.10$, df=3). Thus relative variability did not differ significantly between the cue-tests.

2.3 Inter-year comparisons

2.3.1 Test performances comparisons

Since the protocol presented in 1991 and 1992 differed slightly inter-year comparisons of test performances were carried out in order to reveal possible differences in learning rates (Table 5.4, Fig. 5.1). In 1991 the Pre-test cue-pot contained a food-pellet whereas in 1992 it contained a ping-pong ball. Despite this difference in the protocol, there was no significant difference between the different Pre-test performances of 1991 and 1992 (Mann-Whitney *U*, P=0.81). Although the substrate in the pot was changed from sand in 1991 to clay in 1992 for the Texture-test, there was no significant difference between performances of 1991 and 1992 (Mann-Whitney *U*, P=0.25). The performances in the other non-modified Contrast-test and Olfaction-test did not differ significantly between 1991 and 1992 (Mann-Whitney *U*, respectively P=0.75 and P=0.27).

Table 5.4. Comparisons between the performances (number of trials to 80% success rate) of raccoons in 1991 and 1992 in the different tests: Pre-test (PRE); Contrast-test (CONT); Texture-test (TEXT); and Olfaction-test (OLF). With median number of trials to 80% success rate (MED), range (R), sample size (n), and associated probability (P) (Mann-Whitney *U*).

TEST	1991			1992			P
	MED	R	n	MED	R	n	
PRE	75.0	84	6	78.0	83	6	0.81
CONT	45.0	45	5	45.0	45	5	0.75
TEXT	105.0	30	5	120.0	50	5	0.25
OLF	30.0	10	5	32.5	5	4	0.27

Level of significance $\alpha=0.05$

2.3.2 Variance comparisons

The modifications of the protocol between years had no effect on variances ($P \geq 0.65$) (Table 5.5). Therefore the differences in the protocol did not affect the performances or the variability.

3 DISCUSSION

3.1 Cues

As expected, the tactile discrimination of compaction was learned faster than the visual discrimination. But the 1992 data analysis revealed that the urine olfactory discrimination was learned as fast as the tactile discrimination. Olfactory and tactile cues appeared to be learned equally fast and therefore these cues might have a dominant role in nest detection.

The tactile sensitivity and learning abilities of raccoon are well known. Behavioral experiences involving touch revealed the dexterity of raccoon forepaws (Cole 1907; Davis 1907; Lyall-Watson 1963; Rensh and Dücker 1963) and their associated developed sensory and motor neural structures (Welker and Seidenstein 1959; Welker and Campos 1963; Welker et al. 1964; Zollman and Winkelmann 1962; Pubols et al. 1965, 1971; Turnbull and Rasmusson 1986; Rasmusson and Turnbull 1986; Ray and Doetsch 1990). However the potential of this tactile cue in nest localization is rather limited when considering the large area turtles can use for nesting. It might be of higher value in the case of close clumped nests and for proximate localization. In nest localization, olfactory cues might be more efficient than tactile cues. Indeed olfaction as a distance sense (Österholm 1966; Wells and Lehner 1978; Wells 1978) could allow detection at long distance ("near location" cue of Österholm, 1966), especially fresh nests.

Data on visual discrimination were more difficult to analyze but the texture (Texture-cue) seemed to be of low value as it was associated with the highest number of trials of all tests in both years, despite the different substrate used. At the group level, the performances in the Contrast-test were significantly higher than in the Olfaction-test in 1991, but at individual levels the performances were identical for subjects R3 in 1991, R8 and R10 in 1992 (Appendix 1). So this visual nest cue might have to be considered as a potentially important cue particularly when the visual contrast is at its maximum in fresh nests. Raccoon activity starts at sunset, or

Table 5.5. Variance comparison between raccoons 1991 and 1992 in the Pre-test and the different cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). Variance (S_2), sample size (n), the test statistic T (minimum) and associated probability (P) (Squared ranks test for variances).

TEST	1991		1992		T	P
	S^2	n	S^2	n		
PRE	932.3	6	884.3	6	311.0	0.86
CONT	382.5	5	357.5	5	170.5	0.68
TEXT	142.5	5	520.0	5	155.0	0.65
OLF	12.5	5	8.3	4	156.5	0.95

Level of significance $\alpha = 0.05$

sometimes before (Bider et al. 1968; Shirer and Fitch 1970; Gauthier 1971), and even in daylight (Ivey 1948; Kaufmann 1982) coinciding with the time when some nests have just been laid by turtles (Legler 1954; Mahmoud 1968; Hammer 1969; Petokas and Alexander 1980; Congdon et al. 1983,1987; Congdon and Gatten 1989). Furthermore this visual cue should not be neglected as research on raccoon sight has revealed good performance in visual discrimination tests (Michels and Brown 1959; Michels and Pustek, Jr. 1961), performing as well as gray squirrels (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*), two diurnal species, in a shape discrimination learning experiment (Hitchcock et al. 1963). It appears that the retina of the raccoon has a good cone sensitivity in relatively high light intensity, closer to a diurnally-adapted than a nocturnally-adapted animal (Jacobs and Deegan II 1992). Like the olfactory cue, a visual cue could be detected at some distance from the nest.

My experiments were done under red light, simulating more sunset light conditions rather than complete darkness. An experiment recording visual discrimination at different light intensities would help in assessing the potential importance of these visual cues in turtle nest predation in relation to the diel activity of raccoon.

3.2 Learning

Four different sensory discrimination tests involving the use of three senses (e.g. sight, olfaction and touch) certainly limited the inter-problem transfer of learning sets from one test to another. In fact no correlation was found in both years between the Pre-test and the Contrast-test performances which indicates the relative independence of at least these tests. Shell and Riopelle (1957) using raccoons in visual discrimination tasks, observed intra-problem and inter-problem improvement and formation of learning sets. However in their experiment, 345 different visual problems were presented to the subjects, with more than 50 trials/day/animal. In my experiment, Contrast-test and the Texture-test were two visual tests performed in a row. This could have facilitated the inter-problem transfer which could be reflected by a marked decrease between the coefficients of variation of these cue-tests. This difference was significant in 1991 but not in 1992, and there was no inter-year difference in variances. Overall more trials were necessary to learn the texture than the contrast discrimination, even though the Texture-test was performed after the Contrast-test and the Pre-test. Therefore comparisons and conclusions on cues are relevant even if this trend in the reduction of inter-individual variability (not significant in 1992 but some significant differences in 1991) could reflect in part the familiarisation of the raccoons with the procedure (Riopelle 1953). Indeed Wells and Lehner (1978) observed a similar trend in sensory perception experiments with coyotes involving sight, audition and olfaction. The lowest inter-individual variability was associated with the best performances, in their case in the visual test. Thus the lowest inter-individual variability in the Olfaction-test and the Compaction-test could reflect the species-specific natural propensity of raccoon to use particular senses, that of olfaction and touch.

4 CONCLUSION

Considering the cues tested in these experiments, a hierarchy based on the cue-test performances could be established, however it may not reflect correctly how they could be used by the predator in the wild. The tactile cue was learned quickly but its practical value is reduced by the low probability to detect a nest in a large nesting area using only touch. The olfactory cue discrimination appeared to be learned as fast as the tactile cue discrimination. Olfactory nest cues might have a major role in turtle nest predation, allowing detection at a distance. Vision could have a role in turtle nest predation as this sense appeared well developed in raccoons. In fact this species seems to be well adapted for nocturnal foraging with a developed touch sense and apparently good use of olfaction (Eisenberg and Leyhausen 1972; Stoddart 1980), as well as for daylight foraging with a diurnally-adapted sight (Jacobs and Deegan II 1992).

CHAPTER VI - ADULT SKUNKS

1 INTRODUCTION

Skunks were slow to tame and it was particularly necessary to have their cooperation as they were not descented. In 1991 they refused to come out of their boxes in my presence for days, even when given little food. Because of this slow rate of taming, there was only enough time left to run the Pre-test before the autumn cold and preparation of the animals for overwintering. Subjects S2, S4 and S5 had not learned the Pre-test after more than 253 trials in 51 days. The animals tended to visit other pots after eating the food-pellet at the cue-pot and before coming back to the rest-box to receive their reward. Considering this slow rate of conditioning and the difficulty to adjust the diet in order to "motivate" these animals, modifications were added in the following seasons. In 1992 and 1993, I captured new animals and changed the protocol of the Pre-test, replacing the food pellet in the cue pot by a ping-pong ball. This modification was intended to favor their return to the rest-box to get their food-reward after visiting the cue-pot. In addition the ping-pong ball had the shape and color of an egg, and I wanted to see how the subjects would react to it.

2 RESULTS

2.1 Reaction to ping-pong ball

Skunks reacted to the ball first by smelling it, and then often by touching and pushing the ball with their snout (Table 6.1). Touching with the forepaws was observed by seven of nine individuals but did not occur frequently during the Pre-test and was generally performed later than the other actions. No individuals bit the ball in the first trial but three subjects (S7, S8, and S11) bit the ball in the second trial. This could indicate that these skunks were familiar with "eggs" and were possibly lured by the ping-pong ball in comparison with the other individuals which bit the ball later or not at all.

Table 6.1. Behavior of adult skunks toward the ping-pong ball in the Pre-test indicating the trial number (day number in brackets) when for the first time the subject: smelled the ball (S); touched the ball with the front paw(s) (T); pushed the ball with the "nose" (N); bit the ball (M).

SUBJECT	SMELL (S)	TOUCH (T)	PUSH (N)	BITE (M)
S6	2 (2)	6 (2)	2 (2)	-
S7	1 (1)	1 (1)	1 (1)	2 (2)
S8	1 (1)	-	3 (2)	2 (2)
S9	1 (1)	-	6 (2)	5 (2)
S10	1 (1)	7 (2)	2 (1)	4 (1)
S11	2 (2)	6 (2)	7 (3)	2 (2)
S12	1 (1)	10 (3)	1 (1)	8 (3)
S13	1 (1)	4 (2)	1 (1)	-
S14	1 (1)	47 (11)	2 (1)	47 (11)

2.2 Tests

Individual performances in the different tests are presented in Appendixes 2 and 3.

2.2.1 Sex differences

There was no significant difference between performances of males and females in the first Pre-test (Mann-Whitney *U*, $P=0.84$ $n_{♂}=5$, $n_{♀}=2$) and the first visual Contrast-test (Mann-Whitney *U*, $P=0.34$ $n_{♂}=4$, $n_{♀}=2$). As well there was no significant difference between sexes in the Texture-test (Mann-Whitney *U*, $P=0.68$ $n_{♂}=2$, $n_{♀}=2$) and the Olfaction-test (Mann-Whitney *U*, $P=0.44$ $n_{♂}=2$, $n_{♀}=2$). In the Compaction-test no statistical test was run but the performance of the male S13 (65 trials) was included in the performance interval [65,85] of the females. As a result male and female data were pooled in all analyses (Table 6.2, Fig. 6.1).

2.2.2 Pre-test and Contrast-test

2.2.2.1 Pre-test 1/ Contrast-test 1

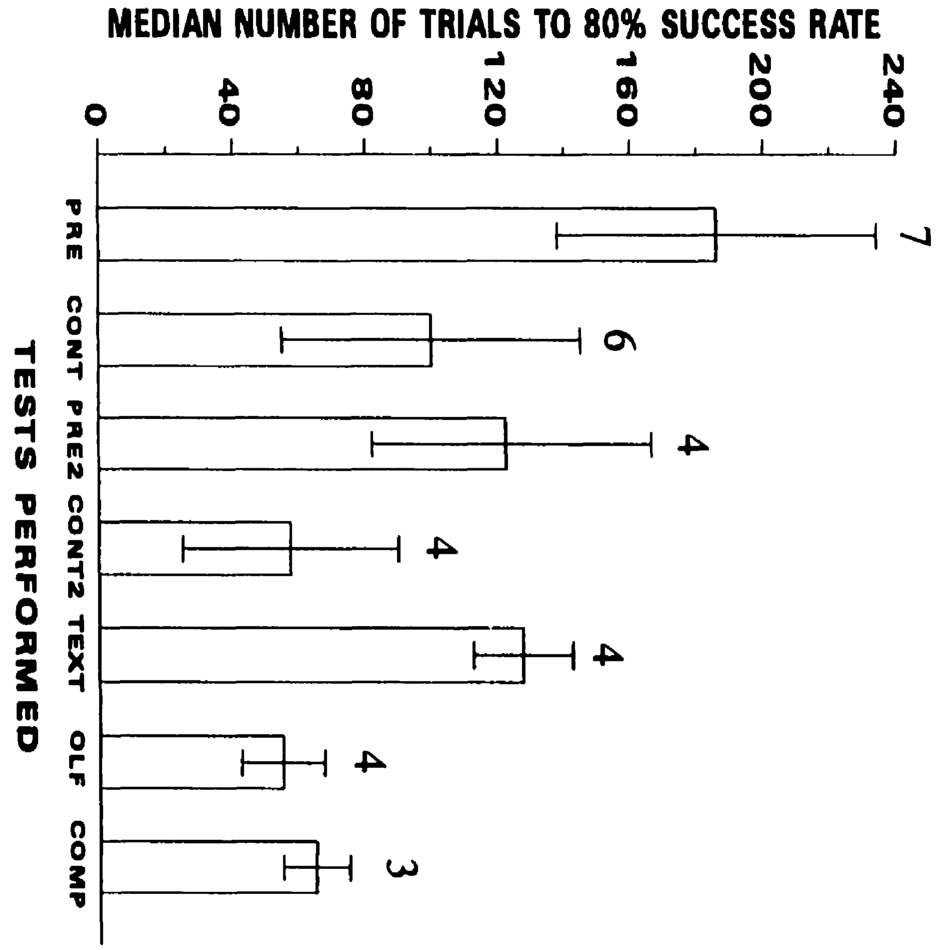
There was a slightly significant decrease in the number of trials to 80% success rate between the first Pre-test and the first Contrast-test (Wilcoxon signed-ranks test, $P<0.04$, $n=6$) but no significant correlation ($r_s=-0.32$, $P>0.50$) which can be explained by a high inter-individual variability in the magnitude of the improvement between these tests (Appendixes 2 and 3). The first Pre-test (CV=24.1%) and the first Contrast-test (CV=36.9%) were not significantly different in relative variability (variance of performance logarithms) (Squared ranks test for variances, $P>0.10$). In fact in the Pre-test the minimum was 130 trials to 80% success rate (subject S8) and the maximum 226 trials (subjects S13 and S14) and in the first Contrast-test the minimum was 65 trials (S13 and S14) and the maximum 155 trials (S10). Therefore, performances in the Pre-test and the Contrast-test were relatively independent.

As mentioned before, some of the individuals of 1992 were kept and used again in 1993 (S10, S11, S12, S13, sample SI). In 1993, these subjects were submitted a second time to the Pre-test and the Contrast-test. The effect of this repeated training is analysed in the following sections.

Table 6.2. Adult skunk mean performance (number of trials) to 80% success rate (MEAN), standard deviation (SD), standard error (SE), and coefficient of variation (CV=SD/MEAN, expressed in percentage) in the different tests: Pre-test performed a first time (PRE1); Pre-test performed a second time (PRE2); Contrast-test performed a first time (CONT1); Contrast-test performed a second time (CONT2); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP).

TEST	SAMPLE	n	MEAN	SD	SE	CV
PRE1	SIV	7	182.6	44.1	16.7	24.1
	SI	4	184.2	48.6	24.3	26.4
CONT1	SIII	6	102.5	37.8	15.4	36.9
	SI	4	117.5	38.0	19.0	32.3
PRE2	SI	4	106.0	38.6	19.3	36.5
CONT2	SI	4	57.5	30.1	15.0	52.4
TEXT	SI	4	126.2	16.0	8.0	12.7
OLF	SI	4	56.2	11.1	5.5	19.7
COMP	SI	3	71.7	11.5	6.7	16.1

Figure 6.1. Skunk median performances (number of trials) to 80% success rate in the Pre-test and the cue-tests: Pre-test performed a first time (PRE); Pre-test performed a second time (PRE2); Contrast-test performed a first time (CONT); Contrast-test performed a second time (CONT2); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). Vertical lines represent range. Number above each bar is the sample size.


MEDIAN NUMBER OF TRIALS TO 80% SUCCESS RATE
0
40
80
120
160
200
240
PRE
CONT
PRE2
CONT2
TEXT
OLF
COMP
7
6
4
4
4
4
3
TESTS PERFORMED

2.2.2.2 Pre-test 2/ Contrast-test 2

There was no significant difference between performances of the Pre-test 2 and the Contrast-test 2 (Wilcoxon signed-ranks test, $P=0.14$, $n=4$). There was a decrease in the number of trials for subjects S10, S12, S13 and an increase for subject S11. There was no significant correlation between these performances ($r_s=-0.32$, $P>0.50$), which is also explained by a high inter-individual variability in the magnitude of the difference between the performances (Appendix 3). There was no significant difference in relative variability between the Pre-test 2 (CV=36.5%) and the Contrast-test 2 (CV=52.4%) (Squared ranks test for variances, $P=0.39$).

2.2.2.3 Pre-test 1/ Pre-test 2

There was a marginally significant trend in improvement in the Pre-test between 1992 and 1993 (Wilcoxon signed-ranks test, $P=0.068$, $n=4$), with all individuals showing better performance in 1993 (Appendixes 2 and 3). However there was no significant correlation between year performances ($r_s=-0.7$, $P>0.20$). Therefore the general trend was an improvement of the learning rate but varying in magnitude from one subject to another one. Also coefficients of variation in the Pre-test 1992 (CV=26.4% $n=4$, sample SI) and 1993 (CV=36.5% $n=4$) were associated with no significant difference in relative variability (Squared ranks test for variances, $P=0.45$).

2.2.2.4 Contrast-test 1/ Contrast-test 2

There was also a marginally significant trend in improvement in the Contrast-test performance between 1992 and 1993 (Wilcoxon signed-ranks test, $P=0.068$, $n=4$), with all individuals showing better performance in the second year (Appendixes 2 and 3). Despite this apparent improvement, there was no significant correlation between 1992 and 1993 performances ($r_s=0.4$, $P>0.50$), which would indicate an inter-individual variability in the magnitude of the improvement in the Contrast-test. This variability was reflected by a relatively high coefficient of variation in 1992 (CV=36.9%, $n=6$) and 1993 (CV=52.4%, $n=4$) Contrast-tests, but with no significant difference between years (Squared ranks test for variances, $P=0.16$).

2.2.3 Inter cue-test comparisons

In order to assess the possible impact of the repeated training in the Pre-test and the Contrast-test on performances in subsequent cue-tests, sample SI (n=4) and sample SII (n=2) were compared. Sample SII consisted of subjects S8 and S14 which performed only once in the Pre-test and the Contrast-test, and were not submitted to the Texture-test. There was no significant difference between performances of these samples in the Olfaction-test (Mann-Whitney *U*, P=0.24).

Of course the small sample sizes limit the reliability of this comparison. But these results would indicate that the double-training affected only the performances in the tests performed twice (Pre-test and Contrast-test) but not the performance in at least the Olfaction-test. Moreover, the subjects of sample SII had not performed in the Texture-test. Thus this absence of a significant difference would also suggest that the number of tests performed in this experiment would not significantly affect the performances of an individual in further different tests.

2.2.3.1 Analysis of variance by ranks

In the following inter cue-test comparisons, performances in the Contrast-test 1992 (performed first) and performances in the other cue-tests (Texture; Olfaction; Compaction) were used. In order to use as much data as possible, the analysis was done in two steps. First I used the data from three cue-tests (Contrast 1; Texture; Olfaction) with four individuals (sample SI), and second I used the data from the four cue-tests (Contrast ; Texture; Olfaction; Compaction) with only three individuals since the subject S10 did not perform the Compaction-test and a same number of data in each treatment was required.

The Friedman two-way ANOVA comparing success in three cue-tests (Contrast 1; Texture; Olfaction) indicated significant differences ($T_2=9$, $P<0.025$ $n=4$). A multiple comparison test ($\alpha=0.05$, $|R_j-R_i|>3.17$, df=6) indicated that the best performances were obtained in the Olfaction-test (Olfaction/ Contrast, $P<0.01$; Olfaction/ Texture, $P<0.01$), whereas performances in the Texture-test and the Contrast-test were poorer and similar to each other (Contrast/ Texture, $P>0.9$).

The Friedman two-way ANOVA comparing success in four cue-tests (Contrast 1; Texture; Olfaction; Compaction) were also significant ($T_2 = 12.5$, $P < 0.01$ n=3). A multiple comparison test ($\alpha = 0.05$, $|R_j - R_i| > 3.45$, df=6) indicated that the best performances were obtained in the Olfaction-test (Olfaction/ Texture, $P < 0.002$; Olfaction/ Contrast, $P < 0.005$; Olfaction/ Compaction, $P < 0.05$). Performances were smaller in the Compaction-test than in the Texture-test (Compaction/ Texture, $P < 0.02$) but similar to the performances in the Contrast-test ($P > 0.05$). Performances in the Texture-test and the Contrast-test were not significantly different ($P > 0.20$).

To summarize, the best performances were obtained in the Olfaction-test. The performances in the Compaction-test were intermediate and close to performances in the Contrast-test 1, which were, along with the Texture-test the worst.

2.2.3.2 Relative variability

When comparing the relative variability between the Contrast-test 1 (CV=32.3%), the Texture-test (CV=12.7%), the Olfaction-test (CV=19.7%), and the Compaction-test (CV=16.1%) from sample SI (n=4) there was no significant difference (Squared ranks test for several variances, $T_2 = 2.935$, $P > 0.25$, df=3). When comparing relative variability between the Contrast-test 2 (CV=52.4%) (instead of the Contrast-test 1) and the other cue-tests, all performed in 1993, there were significant differences between variances of performance logarithms (Squared ranks test for several variances, $T_2 = 10.53$, $P < 0.025$, df=3). The multiple comparison test indicated significant differences between the Contrast-test 2 and the other cue-tests ($P < 0.002$), but no significant differences between the Texture-test, Olfaction-test and Compaction-test ($P > 0.20$).

The coefficient of variation fluctuated during the experiments but tended to decrease between the Contrast-test 2 (CV=52.4%) and the following cue-tests.

3 DISCUSSION

3.1 Cues

The results obtained support the prediction that the olfactory cue discrimination would be learned the fastest. This agrees with previous studies showing the importance of the olfactory sense in the foraging behavior of skunks (Langley 1979; Nams 1991). As reported by Nams (1991), skunks react very strongly to the smell of food, moving their nose back and forth on the ground or sticking their nose in the air and walking straight to the food item. Carr (1974) also observed the pushing of prey with the nose that he referred as nosing. This parallels the consistent reaction of the subjects pushing the ping-pong ball with their snout. Skunks also burrow with part of their snout to catch subterranean prey (Stegeman 1937; Nams 1991). Thus olfactory nest cues might play a major role in turtle nest localization by skunks. In his study on predatory behavior of skunks, Carr (1974) also concluded that skunks had a good sense of smell compared to vision. Indeed, in my experiments, performances in the visual tests (Contrast-test and Texture-test) were worse than in the olfaction test, with the Texture-test presenting the highest number of trials to achieve 80% success, close to the Contrast-test. In a brain anatomy study, Pilleri (1960) observed that compared to mink, skunk had a more developed olfactory system and less developed optic system. Langley (1979) observed that skunks preferred auditory over visual cues to find moving prey. All this suggests that the potential visual nest cues tested here, especially the ground texture, would be of low value in turtle nest detection by skunk, compared to olfactory stimuli. These results lend support to the hypothesis that nocturnal mammal predators use more olfactory and auditory cues than visual cues (Eisenberg and Leyhausen 1972; Stoddart 1980).

The performances in the tactile Compaction-test were worse than in the Olfaction-test, but similar to performances in the Contrast-test and better than performances in the Texture-test. Skunks seem to use their forepaws for different activities like digging for food, rubbing and rolling of prey (Carr 1974). Langley (1979) suggested that olfactory and tactile cues played a role in prey detection when sight and hearing were of no use. The tactile sense in skunks could have an important role in foraging and certainly needs more investigation. However in turtle nest localization, the value of the tactile cue, compared to olfactory distance-cue, would be reduced by the large area turtles can use for nesting.

3.2 Learning

Repeated training in the Pre-test and the Contrast-test resulted in an improvement of the performances in these tests when performed a second time 11 months later, but no difference in variability. It seems that this double training had no detectable effect on the subsequent cue-tests as indicated by the absence of difference between performances of subjects (from sample SI and SII) submitted to different protocols. Inter-problem transfer of learning sets could be reflected by a decrease of the inter-individual variability along the experiment (Riopelle 1953). There was no difference in relative variability between Pre-tests and Contrast-tests, nor between the Contrast-test 1 and the other cue-tests. However marked differences between coefficients of variation of the Contrast-test 2 and the other cue-tests were significant. This decrease of the relative variability could reflect a certain familiarisation of the subjects with the procedure. Overall the limited number of tests associated with the change in the sense tested certainly limited the inter-problem transfer. In experiments by Doty et al. (1967), skunk performances continued to improve even after performing in over 500 visual discrimination problems. They also reported a lower inter-problem transfer in skunk compared to mink, and ferret (*Mustela furo*) submitted to the same tasks. This low learning rate in visual discriminations could be related to poor visual abilities in skunk.

4 CONCLUSION

Olfaction appeared to play a major role in turtle nest predation by skunk in that it can allow perception at a distance from the nest. The role of visual cues, especially soil texture, would be limited as they are associated with the worst performances. Touch in skunk is certainly not to be neglected but its role in turtle nest predation overall might be limited. These results support the hypothesis that olfaction would be more important than sight to this nocturnal mammalian predator.

CHAPTER VII - ADULT RACCOONS AND SKUNKS

1 INTRODUCTION

To proceed to the inter-species comparison, data from 1992 for raccoons (Appendix 1) and sample SI and SIV (Appendix 2 and 3) for skunks were used. All these animals were submitted to the same Pre-test procedure with a ping-pong ball and the same Texture-test (clay), Olfaction-test and Compaction-test. However some of the skunks (sample SI) performed twice in the Pre-test and the Contrast-test, with an improvement when performing the second time. There were some indications that for both species the successive tests were relatively independent when performed for the first time. In other words, performance in a discrimination test presented for the first time was not significantly affected by the test performed previously. Therefore it appeared reasonable to proceed to these data comparisons, using performances from the first Pre-test (Pre-test 1) and Contrast-test 1 (referred to as Contrast-test in this chapter) for the skunks. Performances of these two species were analyzed at two levels. In order to compare the differences in nest cue detection, or relative importance of each cue for each species, data were transformed into ratios (Material and Methods; Appendixes 4.a.b., 5.a.b.). These ratios were used to escape the species-specific effect on the learning rate. Following these performance ratios comparisons, interspecific comparisons of performances (number of trials to 80% success rate in a test) were realized to reveal possible species differences of learning ability in the Pre-test and the different cue-tests.

2 RESULTS

2.1 Performance ratios

The comparison of the performance ratios was conducted in two steps to maximize sample sizes. First I used ratios based on subject performances in three cue-tests (Contrast, Texture, Olfaction) with 1992 sample (n=4) for the raccoons (Appendix 4.a.) and sample SI (n=4) for the skunks

(Appendix 5.a.). Then, I used ratios based on subject performances in four cue-tests (Contrast, Texture, Olfaction and Compaction) with the same raccoon sample (Appendix 4.b.) but a smaller sample for skunk (n=3) (Appendix 5.b.).

2.1.1 Performance ratios with three cue-tests

The comparison of performance ratios (Table 7.1, Fig. 7.1.a) indicated that in the Contrast-test, raccoons learned significantly faster than skunks (Mann-Whitney *U*, P=0.043). In the Texture-test, skunks learned faster than raccoons (Mann-Whitney *U*, P=0.043). Finally, in the Olfaction-test, raccoons and skunks learned equally fast showing no significant difference between performance ratios (Mann-Whitney *U*, P=0.561).

2.1.2 Performance ratios with four cue-tests

The comparison of performance ratios using four cue-tests (Table 7.2, Fig. 7.1.b) indicated that in the Contrast-test, in contrast with the previous comparison of performance ratios using three cue-tests, raccoons and skunks learned at the same rate with no difference in performance ratios (Mann-Whitney *U*, P=0.077). In the Texture-test, skunks again learned faster than raccoons obtaining significantly lower performance ratios (Mann-Whitney *U*, P<0.032). In the Olfaction-test, raccoons and skunks learned equally fast with no significant difference between performance ratios (Mann-Whitney *U*, P=0.86) similar to performance ratios based on three cue-tests. Finally, in the Compaction-test, raccoons learned faster than skunks by having significantly lower ratios (Mann-Whitney *U*, P=0.032).

To summarize, raccoons and skunks learned at the same rate in the Olfaction-test, with both species exhibiting low performance ratios. In the Contrast-test and the Compaction-test, raccoons learned faster than skunks, whereas skunks learned faster than raccoons in the Texture-test.

2.2 Performances

Comparisons of performances between raccoons and skunks (Table 7.3, Fig. 7.2) gives some indication of the interspecific difference of learning rate in the different tests.

Table 7.1. Comparison of performance ratios between raccoons and skunks in three cue-tests Contrast-test (CONT); Texture-test (TEXT); and Olfaction-test (OLF). With sample median (MED), sample range (R), sample size (n), and associated probability (P) (Mann-Whitney *U*).

TEST	RACCOON			SKUNK			P
	MED	R	n	MED	R	n	
CONT	19.29	15.69	4	40.90	13.73	4	0.04
TEXT	63.81	19.62	4	42.13	11.18	4	0.04
OLF	16.90	3.94	4	19.42	7.47	4	0.56

Level of significance $\alpha=0.05$

Table 7.2. Comparison of performance ratios between raccoons and skunks in four cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). With sample median (MED), sample range (R), sample size (n), and associated probability (P) (Mann-Whitney *U*).

TEST	RACCOON			SKUNK			P
	MED	R	n	MED	R	n	
CONT	16.69	13.55	4	32.43	10.92	3	0.08
TEXT	54.99	16.10	4	37.84	8.45	3	0.03
OLF	14.60	3.55	4	15.38	5.08	3	0.86
COMP	14.81	3.78	4	21.80	4.84	3	0.03

Level of significance $\alpha=0.05$

Table 7.3. Comparison of performances (number of trials to 80% success rate) between raccoons and skunks in the different tests: Pre-test (PRE); Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). With sample median (MED), sample range (R), sample size (n), and associated probability (P) (Mann-Whitney *U*).

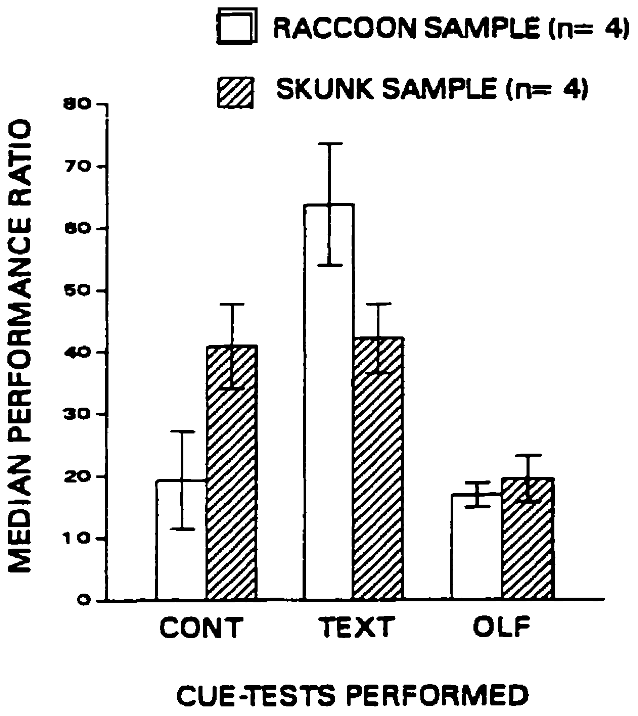
TEST	RACCOON			SKUNK			P
	MED	R	n	MED	R	n	
PRE	78.0	83	6	186.0	96	7	0.003
CONT	45.0	45	5	100.0	90	6	0.017
TEXT	120.0	50	5	127.5	30	4	0.707
OLF	32.5	5	4	55.0	25	4	0.019
COMP	30.0	5	4	65.0	20	3	0.026

Level of significance $\alpha=0.05$

Figure 7.1.a. Median performance ratios of raccoon (n=4) and skunk (n=4) in three cue-tests: Contrast-test (CONT); Texture-test (TEXT); and Olfaction-test (OLF). Vertical lines give range.

Figure 7.1.b. Median performance ratios of raccoon (n=4) and skunk (n=3) in four cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (CCMP). Vertical lines give range.

a


☐ RACCOON SAMPLE (n= 4)
▨ SKUNK SAMPLE (n= 4)
MEDIAN PERFORMANCE RATIO
80
70
60
50
40
30
20
10
0
CONT
TEXT
OLF
CUE-TESTS PERFORMED

b

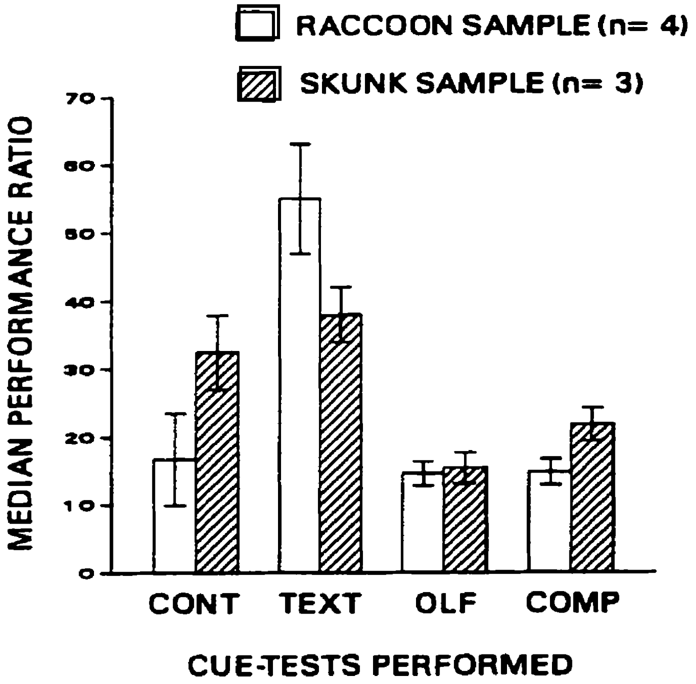
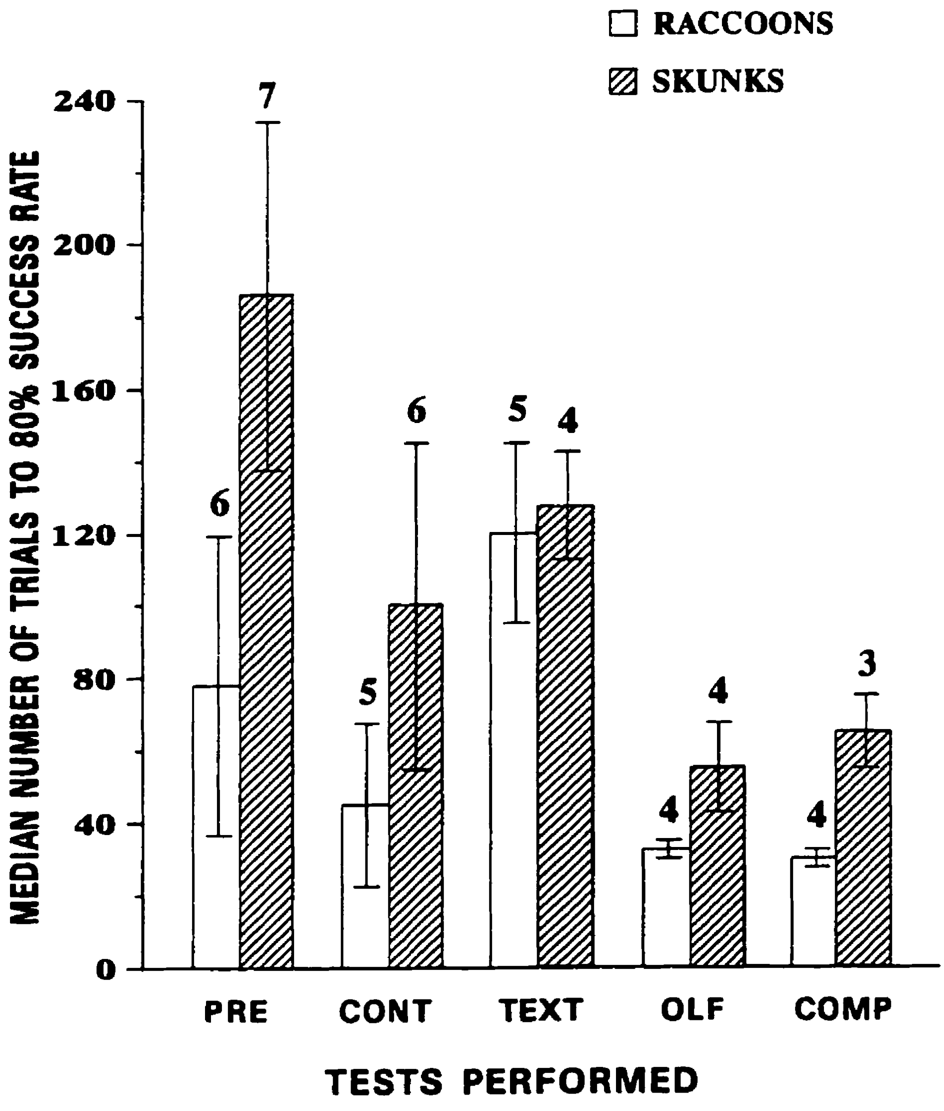

☐ RACCOON SAMPLE (n= 4)
▨ SKUNK SAMPLE (n= 3)
MEDIAN PERFORMANCE RATIO
70
60
50
40
30
20
10
0
CONT
TEXT
OLF
COMP
CUE-TESTS PERFORMED

Figure 7.2. Median performances (number of trials) to 80% success rate of raccoon and skunk in the Pre-test (PRE) and the cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). Vertical lines give range. The number above each bar is the sample size.


☐ RACCOONS
▨ SKUNKS
MEDIAN NUMBER OF TRIALS TO 80% SUCCESS RATE
240
200
160
120
80
40
0
6
7
5
6
5
4
4
4
4
3
PRE
CONT
TEXT
OLF
COMP
TESTS PERFORMED

In the Pre-test and the Contrast-test, raccoons performed significantly better than skunks with smaller number of trials (Mann-Whitney *U*, P=0.003 and P=0.017). In the Texture-test there was no significant difference between raccoons and skunks (Mann-Whitney *U*, P=0.707). In the Olfaction-test and the Compaction-test raccoons performed significantly better than skunks (Mann-Whitney *U*, P=0.019 and P=0.026).

To summarize, except in the Texture-test where both species performed equally poorly, raccoons learned faster than skunks.

2.3 Inter-sample variability

Possible difference between raccoon and skunk sample relative variability (variance of the performance logarithms) was tested, variance comparison being irrelevant due to difference in the magnitude of performance between species. The test was run using data from the Pre-test and the Contrast-test (Contrast-test 1 for skunks), where the protocol was exactly the same for both species with adequate sample sizes. In the Pre-test, no significant difference was found between raccoon (CV=36.4%, n=6) and skunk (CV=24.1%, n=7) relative variability (Squared test for variances, P=0.40). In the Contrast-test as well no significant difference was found between raccoon (CV=40.2%, n=5) and skunk (CV=36.9%, n=6) relative variability (Squared test for variances, P=0.88). There was no significant difference in the Texture-test between raccoon (CV=19.5% n=5) and skunk (CV=12.7%) relative variability (Squared test for variances, P=0.50). However in the Olfaction-test the difference between raccoon (CV=8.9% n=4) and skunk (CV=19.7% n=4) relative variability was significant (Squared test for variances, P=0.024). In the Compaction-test, the relative variability differed significantly between raccoons (CV=8.0% n=4) and skunks (CV=16.1% n=3) (Squared test for variances, P=0.028). The relative variability of raccoon and skunk samples was similar in the first tests but differed in the last Olfaction-test and Compaction-test.

3 DISCUSSION

This project is the first to compare raccoons and skunks in a same behavioral experiment and using discrimination tests involving the use of different senses. It was designed to compare and assess the value of potential turtle nest cues for these species. However, these experiments were based on conditioning which involved learning, and possible difference in information processing between species could have influenced the response of the subjects in the different discrimination tasks. This is one of the problems to be faced in inter-species comparison where, in addition to perceptual organization differences, information processing difference and thus learning could affect the subject's response (Bitterman 1975; Kamil and Yoerg 1982; Zolman 1982). Hence results of the comparisons will be discussed considering this problem.

3.1 Nest-cue perception

The stimuli I used in the experiments were as close as possible, within the constraints of the protocol, to natural stimuli that these animals could confront. As such, results could be relevant to the issue I was looking at, the sensory perception of potential turtle nest cues. This study revealed some interesting aspects of sensory perception and some tendencies emerged in both species.

Raccoon performance ratios were lower than those of skunks in the tactile Compaction-test. This might have been expected, from the proposed hypothesis about predominance of touch sense in raccoons. For olfaction, there was no difference between species. Compared to the other cues tested, olfactory cues seem to be of equivalent importance for both species. Lower performance ratios in skunks might have been expected because of the predominance of olfaction in this species. In any case with the lowest performance ratios obtained in both species, olfaction, at least of urine, would play a major role in turtle nest detection for both skunks and raccoons. With regard to visual nest cues, for both species, the performance ratios were the highest in the Texture-test, but smaller for skunks than raccoons. This confirms the small value of this texture cue especially for raccoons. In the Contrast-test, the difference between ratios was significant based on three cue-tests, and close to significance between ratios using four cue-tests (in part because of a smaller skunk sample size). Smaller performance ratios in raccoons would indicate that this nest-cue has more potential for this species than for skunks. Raccoon sight has been shown to be similar to that of diurnally-adapted foragers (Jacobs and Deegan II 1992) which would rely more on visual information, when compared to nocturnally-adapted carnivores like skunks (Eisenberg and Leyhausen 1972).

3.2 Learning abilities

In the present experiment with discrimination learning involving different senses raccoons performed better than skunks in the Pre-test and three of the cue-tests, except in the Texture-test where performances were not significantly different. Some other differences between raccoons and skunks emerged. In the Pre-test, raccoons seemed not to be affected by the stimulus used, as the performances in 1991 with a food-pellet were similar to the 1992 performances with a ping-pong ball. However for skunks, conditioning was established faster with the ping-pong ball. Skunks could have been less sensitive than raccoons to the reward reinforcement schedule used (i.e. varying the reward size depending of the behavioral response of the subject) particularly in the Pre-test, thus more time being necessary to establish the conditioning. Ough (1979) showed in his experiments that raccoons seemed more sensitive to a food-reward in terms of frequency of items rather than the total quantity (weight). Also lower relative variability of the raccoon sample compared to the skunk sample in the last Olfaction-test and Compaction-test could indicate that the raccoons were more familiar with the procedure (Riopelle 1953).

If looking at previous studies using raccoons or skunks, some disparities and similarities between these species and others were revealed in different discrimination tasks. In an object-discrimination experiment (Doty et al. 1967), skunk performance was situated between ferret and cat performances. In another comparative experiments with three mustelids (ferret, mink and skunk), Doty and Combs (1969) concluded that skunks may be more responsive to position than to object cues whereas the opposite was true for mink and ferrets. In the case of interspecific comparisons, raccoons were better than rats in inter-problem transfer (Fields 1936) and showed similar performances than horses in a reversal learning experiment (Warren and Warren 1962). Raccoons also use more asymmetry cues than squirrels in visual shape discrimination tasks

(Hitchcock et al. 1963), but like cats fail in oddity learning experiments where chimpanzees and monkeys succeed (Strong and Hedges 1966). Overall it is difficult to extract a coherent image of differences between raccoons and skunks in information processing, mainly because objectives and protocols differed between these above studies. Unfortunately this problem is often met when dealing with wild species other than rats and pigeons (Kamil and Yoerg 1982). Considering subject performances in my experiments, it seems that information processing differs between raccoons and skunks.

4 CONCLUSION

For both skunks and raccoons, the olfactory cue would appear to play a predominant role in turtle nest detection. When considering the other performance ratios, raccoons also performed better than skunks with the touch cue and visual contrast cue. As turtle nest predators, raccoons would seem to possess more sensory abilities than skunks at least for the potential nest cues tested. These experiments did not consider the threshold of detection for the different stimuli tested. This latter aspect of sensory perception could reveal interesting differences between the species. For example, comparison of turtle urine threshold of detection between skunks and raccoons would allow us to assess more precisely the potential role of this cue in turtle nest predation for both species. I attempted to do this in 1991 with raccoons and in 1993 with skunks but my apparatus and protocol were not really adapted to do such an experiment. As well a different experimental design would have to be used to investigate and compare information processing between the raccoon and skunk, a design that would have to consider the differences in sensory perception and learning abilities partly revealed in the present project.

CHAPTER VIII - JUVENILE SKUNKS

1 INTRODUCTION

In 1993, two of the captive female skunks, S11 and S12, gave birth to four and five young respectively. One young in each litter died approximately two weeks later and another died at one month of age, leaving three young in each litter. This provided an opportunity to use naïve subjects in my experiments. At the age of 12 weeks, including a four to six week post-weaning period (e.g. Verts 1967), the young were placed in individual pens. I started the experiments a few days later as they were already accustomed to my presence. They were separated in two lots, lot 1 with the individuals L1, L3 and P3, and lot 2 with P1, P2 and L2. Each lot performed the cue-tests in a different order as I wanted to assess the possible effect of the test order of presentation on performances. The visual Texture-test was run last.

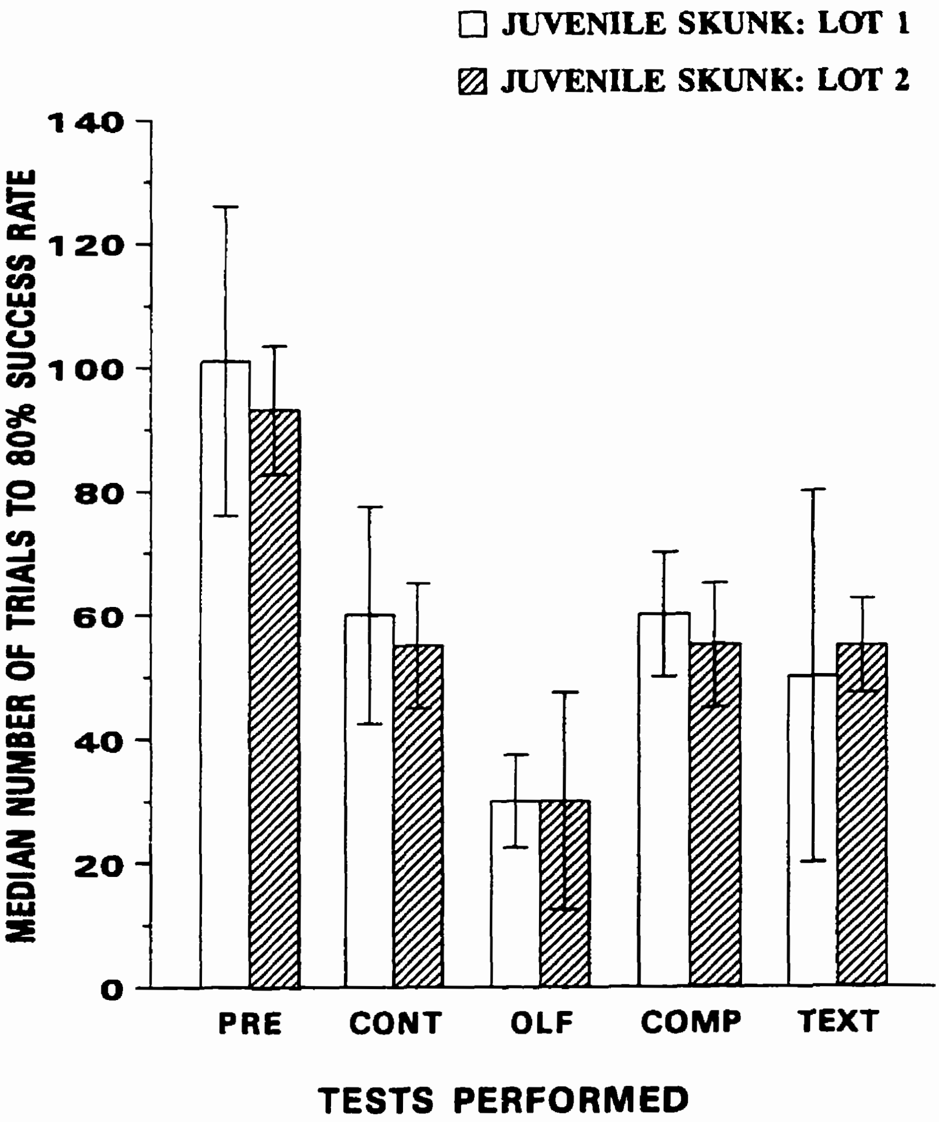
No hypotheses or predictions were proposed for juvenile skunks because of the unknown effect of their neural and physiological stage of development on their performances in the different tests. The experiments were therefore more exploratory first looking at the possible effect of test order of presentation on the performances. Then comparisons with adult skunk performances were designed to reveal possible differences in nest-cue perception and learning abilities between post-weaning young and adults.

2 RESULTS

2.1 Juveniles

As the order of presentation of the cue-tests differed between the two juvenile samples, lot 1 (Compaction, Olfaction, Contrast, Texture) and lot 2 (Contrast, Olfaction, Compaction, Texture) were treated separately in inter-test comparisons and then compared to each other. Performances (number of trials to 80% success rate) of all subjects are presented in Appendix 6 and Fig. 8.1.

Figure 8.1. Median performances (number of trials) to 80% success rate of lot 1 (n=3) and lot 2 (n=3) juvenile skunks in the Pre-test (PRE) and the different cue-tests: Compaction-test (COMP); Olfaction-test (OLF); Contrast-test (CONT); and Texture-test (TEXT). Vertical lines give range.


☐ JUVENILE SKUNK: LOT 1
▨ JUVENILE SKUNK: LOT 2
MEDIAN NUMBER OF TRIALS TO 80% SUCCESS RATE
140
120
100
80
60
40
20
0
PRE
CONT
OLF
COMP
TEXT
TESTS PERFORMED

2.1.1 Inter-test comparisons

2.1.1.1 Lot 1

There was no significant difference between the performances in the Pre-test and the Compaction-test (Wilcoxon signed-ranks test, P=0.109), but this was associated with the lowest probability. It was an extreme case in which all the subjects performed better in the Compaction-test than in the Pre-test (Appendix 6). Furthermore since there was no significant correlation (r_s=-0.5, P=0.33) between performances in the Pre-test and the Compaction-test, this suggests a relative independence between the two tests.

A Friedman two-way ANOVA was run to compare performances in four cue-tests (Compaction; Olfaction; Contrast, Texture). It resulted in no significant difference between cue-test performances (T_2=2.307, n=3, P>0.10). Despite no significant difference, there was a tendency toward a better performance in the Olfaction-test for all subjects compared to the other cue-tests.

2.1.1.2 Lot 2

There was no significant difference between the performances of the Pre-test and the Contrast-test (Wilcoxon signed-ranks test, P=0.109), but again it was associated with the lowest probability. It was an extreme case in which all the subjects presented a better performance in the Contrast-test than in the Pre-test (Appendix 6). Furthermore there was no significant correlation (r_s=-0.5, P=0.33) between the performances in the Pre-test and the Contrast-test suggesting a relative independence between the two tests.

A Friedman two-way ANOVA was run to compare performances in four cue-tests (Contrast, Olfaction, Compaction, Texture). It resulted in no significant difference between the treatments (T_2=0.679, n=3, P>0.25). The subject P1 performed worse in the Olfaction-test and better in the other cue-tests unlike the other two subjects L2 and P2.

2.1.2 Inter-group comparison

There was no significant difference between lot 1 (n=3) and lot 2 (n=3) performances in the Pre-test (Mann-Whitney *U*, P=0.27) which would suggest that the two lots were similar. In order to see if the performance in a cue-test was affected by the number of trials performed previously, performances of the two lots in the Compaction-test and the Contrast-test were compared (Table 8.1), these cue-tests being presented in first or third position depending on the group. There was no significant difference between lot 1 and lot 2 performances in the Compaction-test (Mann-Whitney *U*, P=0.50) and the Contrast-test (Mann-Whitney *U*, P=0.66). In order to determine wether performance in a cue-test was affected by the cue-test performed before in terms of the sense involved, the two lot performances were compared for the Olfaction-test, preceded by the tactile Compaction-test for lot 1 and the visual Contrast-test for lot 2. There was no significant difference between lot 1 and lot 2 performances in the Olfaction-test (Mann-Whitney *U*, P=0.82). When the visual Texture-test was preceded by the tactile Compaction-test for lot 2 and the visual Contrast-test for lot 1 in which the same sense (sight) was involved successively, there was no significant difference between lot 1 and lot 2 performances in the Texture-test (Mann-Whitney *U*, P=0.82).

Furthermore no significant differences were found between lot 1 (n=3) and lot 2 (n=3) variances in the Pre-test, the Contrast-test, the Olfaction-test and the Compaction-test (Squared ranks test for variances, respectively P=0.30, P=0.18, P=0.16, and P=0.25). In the Texture-test, there is a marginally non-significant difference between lots (Squared ranks test for variances, P=0.05) explained by a high number of trials for subject L1 (Appendix 6).

To summarize, at the intra-lot level, there were no differences between the cue-tests. The high learning ability of these growing juveniles resulting in small differences between cue-test performances, could explain this result. Except for individual P1, performances in the olfaction test tended to be better than for the other cue-tests for. For individual P3, performance in the Olfaction-test was as good as in the Contrast-test.

Table 8.1. Performances (number of trials to 80% success rate) comparisons between lot 1 (n=3) and lot 2 (n=3) juvenile skunks in the Pre-test (PRE) and the different cue-tests: Contrast-test (CONT); Compaction-test (COMP); Olfaction-test (OLF); and Texture-test (TEXT). With sample median (MED), sample range (R), and associated probability (P) (Mann-Whitney *U*-test).

TEST	LOT 1		LOT 2		P
	MED	R	MED	R	
PRE	101	50	93	21	0.27
CONT	60	35	55	20	0.66
COMP	60	10	55	20	0.50
OLF	35	15	30	35	0.82
TEXT	50	70	50	15	0.82

Level of significance $\alpha=0.05$

The objective of using the young in two samples was to evaluate the effect of cue-test presentation order on the performances. As no significant difference was found between lot 1 and lot 2 in the different cue-test, it would seem that test presentation order did not affect the performances of the young.

2.2 Comparison with adult skunks

I used samples as large as possible in accordance with the protocol to which the subjects were submitted to compare performances between adults (Appendixes 2 and 3) and juveniles (Appendix 6). The Compaction-test and the Texture-test were not compared statistically because of differences in protocol (order of test presentation, number of tests performed).

2.2.1 Pre-test

As all adults and juveniles were submitted to the same protocol in the Pre-test, sample IV (n=7) for adults and pooled lot 1 and lot 2 (n=6) for juveniles were used. Young skunks performed significantly better than adults (Mann-Whitney *U*, $P<0.005$) (Table 8.2). Due to a difference of magnitude between adult and young performances, relative variability (variance of performance logarithms) instead of variances were compared. In this case no significant difference was found between the relative variability of juveniles (CV=19.9%) and adults (CV=24.1%) (Squared test for variances, $P=0.20$).

2.2.2 Contrast-test

Adults (sample SI+SII, n=6) and juveniles (lot 2, n=3) which performed the Contrast-test first were compared. The performances of young were significantly better than the adults (Mann-Whitney *U*, $P<0.02$) (Table 8.2). Again there was no significant difference in relative variability of juveniles (CV=20.1%) and adults (CV=36.9%) (Squared test for variances, $P=0.10$).

2.2.3 Olfaction-test

Adults (sample SII, n=2) and juveniles (lot 2, n=3) which performed tests in the same order (Pre-test, Contrast-test, Olfaction-test) were compared. There was no significant difference

Table 8.2. Comparison of performances (number of trials to 80% success rate) between juvenile skunk samples (LOT) and adult skunk samples (S) in the Pre-test (PRE), the Contrast-test (CONT), and the Olfaction-test (OLF). With sample size (n), sample median (MED), sample range (R), and associated probability (P) (Mann-Whitney *U*-test).

	JUVENILES				ADULTS				
TEST	LOT	n	MED	R	S	n	MED	R	P
PRE	1+2	6	94.5	51	SIV	7	186.0	96	0.003
CONT	2	3	55.0	20	SIII	6	100.0	90	0.020
OLF	2	3	30.0	35	SII	2	40.0	20	0.767

Level of significance $\alpha=0.050$

between performances of young and adults in the Olfaction-test (Mann-Whitney *U*, P=0.77) (Table 8.2).

3 DISCUSSION

3.1 Nest predation

The fast learning rates of juveniles observed would mean that they could learn to locate turtle nests, especially through olfactory detection of turtle urine, in early life. In the visual Contrast-test the better performances of juveniles (half the magnitude of the adult performances) would indicate that visual information could play a potential rôle in turtle nest localization by skunks in early stages of life. Juveniles start to move with their mother at the age of approximately six weeks (Verts 1967). As most births generally take place between mid April and mid May (Stegeman 1937; Verts 1967; Bailey 1971; Casey and Webster 1975; Wade-Smith and Richmond 1978; Schowalter and Gunson 1982; pers. data), first movements of juveniles with their mothers coincide with the turtle nesting season, lasting approximately from the beginning of June to mid July in North America (Cook 1984; Ernst et al. 1994). Juvenile skunk dispersal takes place generally in August (Verts 1967; Bailey 1971; Bjorge et al. 1981). Six week old young would be able to learn to find turtle nests by following their mother. My young subjects were three to four months old at the time they performed in the first test. Stegeman (1937) observed that at the age of 51 days (approx. 7 weeks), the juveniles were eating anything that their mother was eating, and were digging in the ground for food. As well Carr (1974) noted that captive juveniles only 8 to 9 weeks old, and raised by their mother, already used patterns of predatory behavior similar to those used by adults. Therefore the period during which the young forage with their mother seems to be a very favorable period for them to learn to locate turtle nests.

3.2 Learning

Young skunks performed better than adults in the Pre-test and in the Contrast-test with a rather large difference between group performances. They were 12 weeks old when I separated them from their mother and one week older when they started the tests. It can easily be presumed that they acquired little prior experience in foraging as their food and their enclosure were rather artificial. Thus this difference in learning rate could be explained mostly by their better learning abilities. Carr (1974) had noted the ability of inexperienced young (8 to 14 weeks old), raised with their mothers in captivity, to adapt quite rapidly to new situations consisting of the presentation of different types of prey. In the Olfaction-test, the performances of lot 1 and lot 2 were not different from the other cue-test performances. However four of the naïve juveniles presented better performances in the Olfaction-test than in the other cue-tests, reminiscent of the better performances of the adults in the Olfaction-test compared to the other cue-tests. This result supports the hypothesis that the olfactory sense predominates in skunks, this predominance appearing early in life. In fact Carr (1974) noted that captive juveniles only eight to nine weeks old already used patterns of predatory behavior similar to those used by adults. In addition to the difference of age and development that could explain this difference of learning rates, the fact that the young were born and raised in captivity may have also contributed to their rapid conditioning. Indeed they probably perceived these captive and experimental conditions as their "natural" environment, consequently being more ready to work than the more stressed wild-caught adults.

4 CONCLUSION

The comparison with adults revealed some interesting results with implications for turtle nest predation and the development of sensory abilities. The young appeared to learn faster than the adults which would suggest that turtle nest localization would be easier to learn during youth. Also the juveniles, like the adults, tended to perform better in the olfactory discrimination test than in the other cue-tests, but performed better than the adults in the visual Contrast-test. The behavior of the young evolves continuously resulting in that a same experiment conducted with juveniles differing in age by a few weeks or even days, can produce important disparities in the results (Zolman 1982). Further experiments with younger subjects would certainly contribute to a better understanding of the development of sensory perception and learning in juvenile skunks.

IX. GENERAL DISCUSSION

Stoddart (1980) noted the lack of information on sensory perception for most mammals. Kamil and Yoerg (1982) similarly commented the small number of inter-species comparative studies and the lack of continuity in research on most species with the exception of rats, pigeons and monkeys. They also remarked that most of the studies were rarely related to natural conditions. Recently some failures or limited successes achieved in waterfowl and turtle egg predation control programs, and constraints on the method (use of non-lethal predator control), lead to further research on the predators involved, particularly with raccoons and striped skunks (Nams 1991; Semel and Nicolaus 1992; Larivière, pers. comm. 1994; Tuberville and Burke 1994; Niemuth and Boyce 1995; Pasitschniak-Arts and Messier 1995). My project addressed some of these issues. Instead of studying foraging patterns, it focused on the still poorly understood area of turtle nest sensory perception by the predators. The two main predators of turtle eggs, raccoon and striped skunk were the species of choice for this study.

The total lack of control of the movements of the predators in nature, lead me to use captive animals. After selecting possible cues that the predators might use to locate nests, the objective (and challenge) was to isolate these cues or stimuli in a way allowing discrimination from a neutral stimulus. The tests also had to be simple to replicate. Because of technical constraints, potential tactile moisture cues (difficult to isolate from olfaction), olfactory cues such as excreted egg metabolites, cloacal mucus and female odor (rather difficult to collect and preserve), and auditory cues (hatching noise intensity and frequencies unknown, recording unavailable) among others, were not tested. Finally these experiments considered four potential cues. Interspecific difference in sensitivity to the different cues was unknown, for example, raccoons could have been more sensitive to turtle urine and skunks to turtle female odor. Preliminary experiments in 1990 revealed that both species were able to perceive the stimuli selected. Of course the results obtained do not fully ascertain the use of these cues by raccoons and skunks in the wild. Even though these cues represented only a sample of the cues the animals might be able to perceive, the retained stimuli had the advantage of involving, through the protocol, the separate use of three different senses. Therefore the stimuli were (sensory) indicators allowing an assessment of the differential use of the three senses, olfaction, touch and sight in turtle nest localization.

Protocol

The protocol was designed to assess sensory perception of the two species using non-invasive behavioral observations. The protocol used was based on food-conditioning and discrimination learning using the same subjects in successive tasks. The inter-problem transfer of learning sets that could have resulted was limited by submitting the subjects to four cue-tests involving the use of three different senses separately. Indeed a decrease of relative variability during the experiments was noticed but was not significant for raccoons in 1992 or for adult skunks. Repeating these experiments and changing the order of presentation as attempted with juvenile skunks, would certainly help to assess more precisely the possible effect of inter-problem transfer on performances. Interspecific comparison of behavioral experiments involving learning are open to criticism as information processing might differ between species (Bitterman 1975; Kamil and Yoerg 1982; Zolman 1982). Hence the raccoon's faster rate of learning in almost all of the tests could be the result of the protocol used, favoring the raccoons abilities over that of skunks (Bitterman 1975). The performance of the skunks in the Pre-test depending on the stimulus used (food-pellet or ping-pong ball) compared with the apparent absence of a stimulus effect for raccoons was another example of interspecific difference in information processing. Furthermore captivity and experimental conditions might affect each species in a different way and hence their performances in the tests. Unfortunately these limitations to interspecific comparisons are difficult to circumvent, since the only way would be to conduct numerous behavioral tests in order to understand species-specific information acquisition and processing (an almost infinite process) before doing any interspecific comparison. This disparity in learning rates was circumvented in the treatment of the data by using performance ratios.

As pointed out by Kamil and Yoerg (1982), the protocol influences the behavior of the subjects. However, according to Bitterman (1975):" Learning often involves the differential strengthening of existing behavioral tendencies rather than the establishment of entirely new ones". All things considered, the differences obtained between raccoons and skunks in my experiments could reflect with a certain fidelity natural propensities in sensory perception.

Nest-cues

Raccoons were good in tactile tests, but equally as good in olfactory tests which was not expected. In fact research has focused mostly on their touch sense neuro-anatomy (Welker and Seidenstein 1959; Welker and Campos 1963; Welker et al. 1964; Zollman and Winkelman 1962; Pubols et al. 1965, 1971; Turnbull and Rasmusson 1986; Rasmusson and Turnbull 1986; Ray and Doetsch 1990; among others) and visual discrimination abilities (Munn 1930; Fields 1936; Johnson and Michels 1958a,b; Michels et al. 1960; Hitchcock et al. 1963; Jacobs and Deegan II 1992) neglecting their olfaction (Ferron 1973). In terms of turtle nest localization this result is important because olfactory skills extend the predatory power of raccoons allowing detection from a distance. The visual contrast cue might also be useful in nest searching for raccoons whose retinae structure is close to that of diurnal species (Jacobs and Deegan II 1992) and who tend to rely more on visual information than nocturnal species (Eisenberg and Leyhausen 1972; Stoddart 1980).

In skunks the best performances were obtained in the olfaction-test. This was expected from the results of previous research. Visual cues appeared to be of limited use compared to the other cues tested. However in juveniles, even though four out of six subjects presented better performances in the olfactory cue discrimination, the visual contrast cue and tactile cue were learned relatively fast when compared to adults. In other words, the inter-test differences were low because the learning potential of these growing juveniles was high for all senses, with a predominance in olfaction. It implies that learning of at least olfactory and visual nest cues might be facilitated in young.

Individual experience and learning

It has been suggested that individual foraging experience could explain the high level of turtle nest (Snow 1982) and waterfowl nest predation (Greenwood 1982; Semel and Nicolaus 1992).

Individual experience in foraging includes the use of preferential paths (habitat use and movement patterns) and knowledge of the foraging range. It could also explain the increased risk of predation in the case of clumped nesting habits (Davis and Whiting 1977; Bustard 1979; Hopkins and Murphy 1982; McMurtray 1986) and the nesting site fidelity of some turtle species or populations (Loncke and Obbard 1977; Obbard and Brooks 1980; Talbert et al. 1980; Christens and Bider 1986). These nesting sites could attract local predators on a daily or even yearly basis (McMurtray 1986). However the predator must identify the prey (eggs) as a food item. Indeed, Semel and Nicolaus (1992) installed a feeding station to attract raccoons, during a capture-mark campaign. Chicken eggs were used as bait and it appeared that almost 40% of the individuals failed to prey upon the eggs at least at the first visit to the station. Roy and Dorrance (1992) obtained a similar result in an analogous experiment with striped skunks. These observations would mean that only some subjects recognized these chicken eggs as food. In the case of turtle nests the problem is even more complex for a predator, since the eggs are hidden underground and unattended. Therefore the predator must learn the nest cues which are indirect indices signalling the presence of food, accessible only by digging. Thus it can be assumed that learning would have an important role in proximate turtle nest localization.

Learning abilities of raccoon and skunk

Previous laboratory discrimination experiments and my experiments have shown that adult raccoons (Cole 1907; Davis 1907; Cole and Long 1909; Kitzmiller 1934; Fields 1936; Shell and Riopelle 1957; Johnson and Michels 1958a,b; Thackray and Michels 1958; Michels and Brown 1959; Michels et al. 1960; Johnson 1961; Michels and Pustek, Jr. 1961; Warren and Warren 1962; Strong and Hedges 1966; King et al. 1974; Hitchcock et al. 1963; Lyall-Watson 1963; Rensh and Dücker 1963; Ough 1979) and adult skunks (Doty et al. 1967; Doty and Combs 1969; Carr 1974; Langley 1979; Nams 1991) were able to learn new tasks. In field studies their learning abilities were also tested using the frequency of visits to feeding stations (Dalgish and Anderson 1979) and through aversive conditioning experiments (Conover 1990; Semel and Nicolaus 1992). In the Semel and Nicolaus (1992) experiment some raccoons started to eat eggs, generally broken by other individuals, sometimes only after the sixth visit to the feeding station. In this case these naïve individuals were able to include a new item in their diet by learning, benefiting from experienced individuals. Carr (1974) observed that adult skunks "were able to learn a great deal from one experience with an unusual prey type" and learn rapidly when confronted with a new prey. Also Nams (1991) showed that skunks were able to improve their olfactory search for food with training.

Some of these experiments (Nicolaus et al. 1982; Nams 1991) offered conspicuous food items like chicken eggs, or meat. Sometimes individuals benefited from other experienced ones (Nicolaus et al. 1982; Roy and Dorrance 1992; Semel and Nicolaus 1992). However it seems far less probable that an individual predator alone could learn to find a turtle nest as the presence of eggs is indicated by indirect indices. In a field study by Tuberville and Burke (1994), flag markers posted near turtle nests did not affect predation of these nests by raccoons. These results would indicate that the raccoons had not associated fluorescent plastic flag markers, a very conspicuous but indirect visual cue, with turtle nests.

Both raccoons and skunks are generally solitary foragers (Kaufmann 1982; Wade-Smith and Verts 1982). Even if a naïve individual had the opportunity to find an already predated nest, most of the cues necessary to find another intact nest would be largely disturbed. The possibility that a mature individual learns to locate turtle nests is perhaps better where nests are clumped (Loncke and Obbard 1977; Obbard and Brooks 1980; McMurtray 1986; Eckrich and Owens 1995). Indeed it has been observed, especially for raccoons, that an abundant localized source of food tends to attract numerous individuals (Tevis 1947; Bider et al. 1968; Delorme 1988; Dalgish and Anderson 1979; Nicolaus et al. 1982; McMurtray 1986; Semel and Nicolaus 1992; Eckrich and Owens 1995). In this case it is possible to imagine that a naïve individual benefits from another individual's presence, finding eggs left from previously predated nests, and by chance or imitation (Coussi-Korbel and Fragaszy 1995) finding new nests by foraging in the vicinity. Of course the clumped distribution of nests would increase the chance of being rewarded.

Overall, it seems that the best time for a predator to learn to find turtle nests would be during its youth, when foraging with its mother. Indeed juvenile skunks (three months old) in my experiments appeared to have better learning abilities than adults. Carr (1974) observed that young skunks learned very fast to deal with a new prey. It is also suspected that food preferences are formed during early life (Semel and Nicolaus 1992) as shown with another mustelid, the polecat (*Mustela putorius*) (Apfelbach 1973). The period of foraging with the mother, generally one and a half to two months after birth for skunks (Verts 1967), as well as for raccoons (Schneider et al. 1971; Ricard 1986), coincides with the nesting period of turtles, which takes place in June and the beginning of July in North America, especially in the northern part of their range and Québec (Cook 1984; Ernst et al. 1994). This would give juveniles the best opportunity to learn to find turtle nests by benefiting from an experienced mother. Furthermore in both species females with young generally frequent a small home range, compared to males (Verts 1967; Bider et al. 1968; Schneider et al. 1971; Storm 1972; Fritzell 1978b; Greenwood 1982) and therefore forage more often in the same paths, thus increasing their familiarity with the site and consequently the chance of encountering a nest if the home range embraces a turtle nesting site.

X. PROSPECTS IN CONSERVATION

If the role of learning in nest predation is as important as is indicated and predation is caused by a very few experienced individuals, familiar with their home range (Greenwood 1982; Snow 1982; Semel and Nicolaus 1992), then systematic lethal trapping of a predator population would be a poor control strategy. Furthermore the ecological role of these native predators is not limited to turtle egg predation and these methods of predator control might have an impact at other levels of the ecosystem (Sargeant et al. 1984). Indeed Crabtree and Wolfe (1988) observed that skunks were not searching specifically for eggs (of waterfowl) but that vulnerability of these eggs was dependent on the availability of alternate food sources.

New tools for turtle nest protection ?

To limit nest predation and to protect nests, one method is to find the nests before the predators. This can be achieved by observing nesting females or locating nests using visual cues when patrolling a nesting site. This simple method has proved to be efficient (Bleakney 1963; Landers et al. 1980; McMurtray 1986; Schwarzkopf and Brooks 1987; Congdon et al. 1994; Bider, pers. comm.) but requires a large investment in time. Time could be reduced and success rate of nest finding increased by using a trained dog to locate nests. This technique has been used with success to locate tortoises (Schwartz and Schwartz 1974). However it implies that nests which are found must be protected with screens to avoid having predators find them. To avoid this problem, transplanting the eggs to a safe site was applied with success (Stancyk et al. 1980; Stancyk 1982). This method requires that nests be found in the 48 hours after laying otherwise manipulation of the eggs might have deleterious effects (Bustard 1979; Stancyk et al. 1980). As olfactory cues could play a major role in nest localization, spraying of a substance that neutralises or masks odors or acts as a repellent could deceive the predators. However before implementation more research is needed on olfactory capacities and abilities of the predators involved, particularly to determine their power of odor discrimination. Despite some conflicting results on the effect of rain on turtle nest predation rate (Legler 1954; Hammer 1969; Burger 1977; Wilhoft et al. 1979; Bider, pers. comm.), water could be considered as a potential substance to use. If this method proves effective, it could become a cheap way involving limited labor and facilities (compared to nest site fencing, trapping and relocation of the predators, transplanting eggs, hatcheries) to reduce turtle nest predation. This method certainly would not be perfect and as in most cases the realistic goal would be to reduce nest predation rather than to terminate it completely. Meanwhile aversive conditioning seems to be an interesting avenue despite its failure in a project to reduce sea turtle nest predation (Hopkins and Murphy 1982). The failure was believed to result from simultaneous consumption of treated and non-treated eggs by the predators (raccoon), therefore preventing the formation of an aversive response. It seems that this method could certainly be used with some improvement. Conover (1990) recommended that this method to reduce nest predation has to be implemented before the peak of the nesting season so that most of the predators would not be rewarded by non-treated eggs during the conditioning phase. If considering the long-term, conditioning experiments indicate that there is a learning effect over one year in captive raccoons (Kitzmiller 1934; Rensch and Dücker 1963) and also in skunks. In the wild some of the individuals (raccoons) that developed an aversive response toward eggs, still avoided eggs after one year (Semel and Nicolaus 1992). This method could result in a decrease of nest predation after a few years as only some individuals in the population, the experienced turtle egg eaters, would be targeted. However some interspecific differences in learning abilities and information processing, as revealed by my experiments, might have to be considered before using this method.

Recent reports of long-term studies on turtle populations (Brooks et al. 1991; Congdon et al. 1993, 1994) revealed that the most critical stages to look at in order to maintain a stable turtle population would be mature adults and juveniles (sub-adults). In this condition, egg protection might have little impact on the long-term if no efficient measures are taken to protect juveniles and adults (Brooks et al. 1991; Frazer 1992; Congdon et al. 1993, 1994). Of course there is certainly not one perfect method and nest predation control will have to be achieved through a combination of methods adapted to each situation, considering the practical and financial constraints setting the limits. One recent way to meet these constraints is to take advantage of the landscape such as banning access to nesting sites on a peninsula (Lokemoen and Woodward 1993; Bider, pers. comm.). In fact the ideal solution would be to protect and even restore pristine habitats on the largest possible scale (Angermeier and Karr 1994; Newmark 1995; Sinclair et al. 1995) where turtles have managed to survive and evolved for millions of years despite the pressure of egg predation.

XI. SUMMARY AND CONCLUSION

These experiments provided new information on turtle nest sensory perception by raccoons and skunks. The olfactory cue appeared to be important to both species. Skunks performed best in the olfaction-test as expected. Raccoons performed equally well in the olfaction test and tactile test. The role of the tactile cue, even for raccoons whose touch sense is particularly developed, seems rather limited when considering the large area turtles can use for nesting. Visual cues, at least hue contrast, could be of value to raccoons which performed as well as in the olfaction test and tactile test for some of the subjects. Overall olfaction may have an important role in turtle nest localization by raccoons and skunks, especially as this sense allows detection at a distance. Using raccoons and skunks in a same protocol revealed interspecific differences in learning rates, and thus information processing, raccoons learning faster than skunks in all the tests except in the texture-test where they performed equally poorly. In juvenile skunks, even though the olfactory cue discrimination was learned faster than the other cues by four individuals out of five, the visual contrast cue and tactile cue were learned relatively fast when compared to adults. Learning turtle nest cues would be facilitated for young which hunt with mothers who have learned to find nests.

REFERENCES

Angermeier P. L. and J. R. Karr 1994. Biological integrity versus biological diversity as policy directives. Protecting biotic resources. BioScience 44:690-697.

Apfelbach R. 1973. Olfactory sign stimulus for prey selection in polecats (*Putorius putorius* L.). Z. Tierpsychol. 33:270-273.

Auffenberg W. and J. B. Iverson 1979. Demography of terrestrial turtles. *In* Turtles: perspectives and research. *Edited by* M. Harless and H. Morlock. John Wiley and Sons, Ltd., New-York. pp. 541-570.

Bailey T. N. 1971. Biology of Striped Skunks on a Southwestern Lake Erie Marsh. Am. Midl. Nat. 85:196-207.

Bernays E. A. and W. T. Wcislo 1994. Sensory capabilities, information processing, and resource specialization. Quart. Rev. Biol. 69:187-204.

Bider J. R., P. Thibault et R. Sarrazin 1968. Schèmes dynamiques spatio-temporels de l'activité de *Procyon lotor* en relation avec le comportement. Mammalia 32:137-163.

Bitterman M. E. 1975. The comparative analysis of learning. Science 188:699-709.

Bjorge R. R., J. R. Gunson and W. M. Samuel 1981. Population characteristics and movements of striped skunks (*Mephitis mephitis*) in Central Alberta. Can. Field-Nat. 95:149-155.

Bleakney S. J. 1963. Notes on the distribution and life histories of turtles in Nova Scotia. Can. Field-Nat. 77:67-76.

Bowen B. W., T. A. Conant and S. R. Hopkins-Murphy 1994. Where are they now? The Kemp's ridley headstart project. Conserv. Biol. 8:853-856.

Brooks R. J., G. P. Brown and D. A. Galbraith 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Can. J. Zool. 69:1314-1320.

Burger J. 1977. Determinants of hatching success in Diamonback terrapin, *Malaclemys terrapin*. Am. Midl. Nat. 97:444-464.

Bustard R. H. 1979. Population dynamics of sea turtles. *In* Turtles: perspectives and research. *Edited by* M. Harless and H. Morlock. John Wiley and Sons, Ltd., New-York. pp. 523-540.

Cagle F. R. 1949. Notes on the raccoon, *Procyon lotor megalodous* lowery. J. Mammal. 30:45-47.

Carr D. E. 1974. Predatory behavior in the striped skunk, *Mephitis mephitis*. Ph.D. Thesis, Cornell University, Ithaca. 77pp.

Casey G. A. and W. A. Webster 1975. Age and sex determination of Striped Skunks (*Mephitis mephitis*) from Ontario, Manitoba and Québec. Can. J. Zool. 53:223-226.

Christens E. and J. R. Bider 1986. Reproductive ecology of the painted turtle (*Chrysemys picta marginata*) in southwestern Québec. Can. J. Zool. 64:914-920.

Christens E. and J. R. Bider 1987. Nesting activity and hatching success of the painted turtle (*Chrysemis picta marginata*) in Southwestern Québec. Herpetologica 43:55-65.

Cole L. W. 1907. Concerning the intelligence of raccoons. J. Comp. Neurol. Psychol. 17:211-261.

Cole L. W. and F. M. Long 1909. Visual discrimination in raccoons. J. Comp. Neurol. Psychol. 19:657-683.

Congdon J. D., A. E. Dunham and R. C. van Loben Sels 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoïdea blandingii*): implications for conservation and management of long-lived organisms. Conserv. Biol. 7:826-833.

Congdon J. D., A. E. Dunham and R. C. van Loben Sels 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. Amer. Zool. 34:397-408.

Congdon J. D. and R. E. Gatten, Jr. 1989. Movements and energetics of nesting *Chrysemis picta*. Herpetologica 45:94-100.

Congdon J. D., D. W. Tinkle, G. L. Breitenbach and R. van Loben Sels 1983. Nesting ecology and hatching success in the turtle *Emydoidea blandingi*. Herpetologica 39:417-429.

Congdon J. D., D. W. Tinkle, G. L. Breitenbach and R. Van Loben Sels 1987. Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. Herpetologica 43:39-54.

Conover R. M. 1989. Potential compounds for establishing conditioned food aversion in raccoons. Wildl. Soc. Bull. 17:430-435.

Conover R. M. 1990. Reducing mammalian predation on eggs by using a conditioned taste aversion to deceive predators. J. Widl. Manage. 54:360-365.

Conover W. J. (ed.) 1980. Practical nonparametric statistics (2nd. ed.). Wiley and Sons, New-York. 493pp.

Cook F. R. 1984. Introduction to Canadian Amphibians and Reptiles. National Museum of Canada, National Museum of Natural Sciences. Ottawa. 200pp.

Coussi-Korbel S. and D. M. Fragaszy 1995. On the relation between social dynamics and social learning. Anim. Behav. 50:1441-1453.

Crabtree R. L., L. S. Broome and M. L. Wolfe 1989. Effects of habitat characteristics on gadwall nest-site selection. J. Wild. Manage. 53:129-137.

Crabtree R. L. and M. L. Wolfe 1988. Effects of alternate prey on skunk predation of waterfowl nests. Wild. Soc. Bull. 16:163-169.

Dalgish J. and S. Anderson 1979. A field experiment on learning by raccoons. J. Mammal. 60:620-622.

Daniel W. W. (ed.) 1990. Applied nonparametric statistics (2nd ed.). PWS-KENT Publ. Co., Boston. 635pp.

Davis G. E. and M. C. Whiting 1977. Loggerhead sea turtle nesting in Everglades National Park, Florida U.S.A. Herpetologica 33:18-28.

Davis H. B. 1907. The raccoon: a study in animal intelligence. Amer. J. Psychol. 18:447-489.

Deblinger R. D., J. J. Vaske, and D. W. Rimmer 1992. An evaluation of different predator exclosures used to protect atlantic coast piping plover nests. Widl. Soc. Bull. 20:274-279.

Delorme L. 1988. Intraspecific interactions of raccoons (*Procyon lotor*) at a feeding station. M.Sc. Thesis, Macdonald Campus-McGill University, Ste-Anne-de-Bellevue. 37pp.

Dorney R. S. 1954. Ecology of marsh raccoons. J. Wild. Manage. 18:217-225.

Doty B. A. and W. C. Combs 1969. Reversal learning of object and positional discrimination by minks, ferrets and skunks. Quat. J. Exp. Psychol. 21:58-62.

Doty B. A., L. A. Doty and N. C. Jones 1967. Learning-set formation by mink, ferrets, skunks and cats. Science 155:1579-1580.

Dunn J. P. and J. A. Chapman 1983. Reproduction, physiological responses, age structure, and food habits of raccoon in Maryland, U.S.A. Z. Säugetierkunde 48:161-175.

Dusenbery D. B. (ed.) 1992. Sensory ecology. How organisms acquire and respond to information. W. H. Freeman and Co., New-York. 558pp.

Eckrich E. C. and D. W. Owens 1995. Solitary versus arribada nesting in the Olive Ridley sea turtle (*Lepidochelys olivacea*): A test of the predator-satiation hypothesis. Herpetologica 51:349-354.

Ehrenfeld D. W. 1979. Behavior associated with nesting. *In* Turtles: perspectives and research. *Edited by* M. Harless and H. Morlock. John Wiley and Sons, Ltd., New-York. pp.417-434.

Ehrenfeld D. W. 1982. Options and limitations in the conservation of sea turtles. *In* Biology and conservation of sea turtles. *Edited by* K. A. Bjorndal. Smithsonian Institution Press, Washington, D.C. pp.457-464.

Eisenberg J. F. and P. Leyhausen 1972. The phylogenesis of predatory behavior in mammals. Z. Tierpsychol. 30:59-93.

Ellis R. J. 1964. Tracking raccoons by radio. J. Wild. Manage. 28:363-368.

Erickson A. B. and H. I. Scudder 1947. The raccoon as a predator on turtles. J. Mammal. 28:406-407.

Ernst C. H. 1986. Ecology of the turtle, *Sternotherus odoratus*, in Southeastern Pennsylvania. J. Herpetol. 20:341-352.

Ernst C. H., R. W. Barbour and J. E. Lovich (eds.) 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington and London. 578pp.

Ewert M. A. 1979. The embryo and its egg: development and natural history. *In* Turtles: perspectives and research. *Edited by* M. Harless and H. Morlock. John Wiley and Sons, Ltd., New York. pp. 333-343.

Farrell R. F. and T. E. Graham 1991. Ecological notes on the turtle *Clemmys insculpta* in Northwestern New-Jersey. J. Herpetol. 25:1-9.

Fellows B. J. 1967. Chance stimulus sequences for discrimination tasks. Psychol. Bull. 67:87-92.

Ferron J. 1973. Morphologie comparée de l'organe de l'odorat chez quelques mammifères carnivores. Naturaliste Can. 6:525-541.

Fields P. E. 1936. A comparison of white rats and raccoons with respects to their visual discrimination of certain geometrical figures. J. Comp. Psych. 21:341-355.

Frazer N. B. 1992. Sea turtle conservation and halfway technology. Conserv. Biol. 6:179-184.

Fritzell E. K. 1978a. Habitat use by prairie raccoons during the waterfowl breeding season. J. Wildl. Manage. 42:118-127.

Fritzell E. K. 1978b. Aspects of raccoon (*Procyon lotor*) social organization. Can. J. Zool. 56:260-271.

Gauthier M. C. 1971. The activity of the striped skunk, *Mephitis mephitis* (Shreber), in Québec. M.Sc. Thesis, Macdonald Campus-McGill University, Ste Anne-de-Bellevue. 101pp.

Gibbons W. J. 1968. Population structure and survivorship in the painted turtle, *Chrysemis picta*. Copeia 1968:260-268.

Glueck T. F., W. R. Clark and R. D. Andrews 1988. Raccoon movement and habitat use during the fur harvest season. Wild. Soc. Bull. 16:6-11.

Goodrich J. M. and S. W. Buskirk 1995. Control of abundant native vertebrates for conservation of endangered species. Conserv. Biol. 9:1357-1364.

Grau G. A., G. C. Sanderson, and J. P. Rogers 1970. Age determinaton of raccoons. J. Wildl. Manage. 34:364-372.

Greenwood R. J. 1982. Nocturnal activity and foraging of prairie raccoons (*Procyon lotor*) in North Dakota. Am. Midl. Nat. 107:232-243.

Greenwood R. J. 1986. Influence of striped skunk removal on upland duck nest success in North Dakota. Wild. Soc. Bull. 14:6-11.

Greenwood R. J., P. M. Arnold, and B. G. McGuire 1990. Protecting duck nests from mammalian predators with fences, traps and a toxicant. Wildl. Soc. Bull. 18:75-82.

Gustavson C. R. 1974. Coyote predation control by aversive conditioning. Science 184:581-583.

Gustavson C. R. 1977. Comparative and field aspects of learned food aversions. *In* Learning mechanisms in food selection. *Edited by* Barker L. M., M. R. Best and M. Domjan. Baylor University Press, Waco, Texas. pp. 23-43.

Hamilton W. J. Jr. 1936. Seasonal food of skunks in New-York. J. Mammal. 17:240-246.

Hamilton W. J. Jr. 1940. Observations on the reproductive behavior of the snapping turtle. Copeia 1940:124-126.

Hamilton W. J. Jr. 1951. Warm weather foods of raccoon in New-York State. J. Mammal. 32:341-344.

Hammer D. A. 1969. Parameters of a marsh snapping turtle population Lacreek refuge, South Dakota. J. Wildl. Manage. 33:995-1005.

Hitchcock L. Jr., K. M. Michels and D. R. Brown 1963. Discrimination learning: squirrels vs raccoons. Perceptual and Motor Skills 16:405-414.

Hoffman C. O. and J. L. Gottschang 1977. Numbers, distribution, and movements of a raccoon population in a suburban residential community. J. Mammal. 58:623-636.

Hopkins S. R. and M. T. Murphy 1982. Testing of lithium chloride aversion to mitigate raccoon predation of loggerhead turtle nests. Pro. Ann. Conf. SEAFWA. 36:484-491.

Iverson J. B. 1991. Patterns of survivorship in turtles (Order Testudines). Can. J. Zool. 69:385-391.

Ivey D. W. R. 1948. The raccoon in the salt marshes of Northeastern Florida. J. Mammal. 29:290-291.

Jacobs G. H. and J. F. Deegan II 1992. Cone photopigments in nocturnal and diurnal procyonids. J. Comp. Physiol. A 171:351-358.

Jerison H. J. 1983. The evolution of the mammalian brain as an information-processing system. *In* Advances in the study of mammalian behavior. *Edited by* Eisenberg J. F. and D. G. Kleiman. Spec. Publ. Amer. Soc. Mamm. 7:113-146.

Johnson J. I. Jr. and K. M. Michels 1958a. Learning sets and object-size effects in visual discrimination learning by raccoons. J. Comp. Physiol. Psychol. 51:376-379.

Johnson J. I. and K. M. Michels 1958b. Discrimination of small intervals and objects by raccoons. Anim. Behav. 6:164-170.

Johnson J. I. Jr. 1961. Double alternation by raccoons. J. Comp. Physiol. Psychol. 54:248-251.

Kamil A. C. and S. I. Yoerg 1982. Learning and foraging behavior. *In* Perspectives in ethology 5: Ontogeny. *Edited by* Bateson P. P. G. and P. H. Klopfer. Plenum Press, London. pp. 325-354.

Karl S. A., B. W. Bowen and J. C. Avise 1995. Hybridization among the ancients mariners: characterization of marine turtle hybrids with molecular genetic assays. The J. Heredity 86:262-268.

Kaufmann J. H. 1982. Raccoon and allies. *In* Wild mammals of North America, biology, management and economics. *Edited by* Chapman J. A. and G. A. Feldhamer. The Johns Hopkins University Press, Baltimore. pp. 567-585.

Kelker G. H. 1937. Insect food of skunks. J. Mammal. 18:164-170.

Kennedy M. L., J. P. Nelson Jr., F. W. Weckerly, D. W. Sugg, and J. C. Stroh 1991. An assessment of selected forest factors and lake level in raccoon management. Wild. Soc. Bull. 19:151-154.

King G. D., R. W. Shaeffer and S. C. Pearson 1974. Reinforcement schedule preference of a raccoon (*Procyon lotor*). Bull. Psychonom. Soc. 4:97-99.

Kissel R. E. Jr. and M. L. Kennedy 1992. Ecologic relationships of co-occuring populations of opossum (*Didelphis virginianus*) and raccoons (*Procyon lotor*) in Tennessee. J. Mammal. 73:808-813.

Kitzmiller A. B. 1934. Memory of raccoons- Note. Amer. J. Psychol. 46:511-512.

LaGrange T. G., J. L. Hansen, R. D. Andrews, A. W. Hancock, and J. M. Kienzler 1995. Electric fence predator exclosure to enhance duck nesting: a long-term case study in Iowa. Wildl. Soc. Bull. 23:261-266.

Landers L. J., J. A. Garner, and A. W. McRae 1980. Reproduction of gopher tortoises (*Gopherus polyphemus*) in Southwestern Georgia. Herpetologica 36:353-361.

Langley W. M. 1979. Preference of the striped skunk and opossum for auditory over visual prey stimuli. Carnivore 2:31-34.

Legler J. M. 1954. Nesting habits of the Western Painted Turtle *Chrysemis picta bellii* (gray). Herpetologica 10:137-144.

Lewontin R. C. 1966. On the measurement of relative variability. Syst. Zool. 15:141-142.

Linck M. H., J. A. DePari, B. O. Butler, and T. E. Graham 1989. Nesting behavior of the turtle, *Emydoidea blandingii*, in Massachusetts. J. Herpetol. 23:442-444.

Llewellyn L. M. and F. M. Uhler 1952. The foods of fur animal of the Patuxent Research Refuge, Maryland. Am. Midl. Nat. 48:193-203.

Lokemoen J. T., H. A. Doty, D. E. Sharp and J. E. Neaville 1982. Electric fences to reduce mammalian predation on waterfowl nests. Wild. Soc. Bull. 10:318-323.

Lokemoen J. T. and R. O. Woodward 1993. An assessment of predator barriers and predator control to enhance duck nest success on peninsulas. Wild. Soc. Bull. 21:275-282.

Loncke D. J. and M. E. Obbard 1977. Tag success, dimensions, clutch size and nesting site fidelity for the snapping turtle, *Chelydra serpentina* (Reptilia, Testudines, Chelydridae), in Algonquin park, Ontario, Canada. J. Herpetol. 11:243-244.

Lotus Development Corporation 1983, 1989. Cambridge, MA.

Lotze J. and S. Anderson 1979. Procyon lotor. Am. Soc. Mammal. (Pub.). Mammalian species 119:1-8.

Lyall-Watson M. 1963. A critical re-examination of food "washing" behaviour in the raccoon (*Procyon lotor* LINN.). Proc. Zool. Soc. London 141:371-393.

Macdonald D. W., L. Brown, S.Yerli and A. Canbolat 1994. Behavior of red foxes, *Vulpes vulpes*, caching eggs of loggerhead turtles, *Caretta caretta*. J. Mammal. 75:985-988.

Mahmoud L. Y. 1968. Nesting behavior in the Western Painted Turtle *Chrysemis picta bellii*. Herpetologica 24:158-162.

McCabe R. A. and E. L. Kozicky 1972. A position on predator management. J. Wildl. Manage. 36:382-394.

McClearn D. 1992. Locomotion, posture, and feeding behavior of kinkajous, coatis, and racccoons. J. Mammal. 73:245-261.

McMurtray J. D. 1986. Reduction of raccoon predation on sea turtle nests at Canaveral National Seashore, Florida. CPSU Technical Report 20. University of Georgia. Athens, Georgia. 52 pp.

Mech D. L., D. M. Barnes, and J. R. Tester 1968. Seasonal weight changes, mortality, and population structure of raccoons in Minnesota. J. Mammal. 49:63-73.

Michels K. M. and D. R. Brown 1959. The delayed-response performance of raccoons. J. Comp. Physiol. Psychol. 52:737-740.

Michels K. M., B. E. Fisher and J. I. Johnson Jr. 1960. Raccoon performance on color discrimination problems. J. Comp. Physiol. Psychol. 53:379-380.

Michels K. M. and J. J. Pustek Jr. 1961. The solution of patterned-strings problems by raccoons. J. Comp. Physiol. Psychol. 54:439-441.

Munn N. L. 1930. Pattern and brightness discrimination in raccoons. J. Genet. Psychol. 37:3-33.

Nams V. O. 1991. Olfactory search images in striped skunks. Behaviour 119:267-284.

Nelson R. L. and R. L. Linder 1972. Percentage of raccoons and skunks reached by egg baits. J. Wildl. Manage. 36:1327-1329.

Newmark W. D. 1995. Extinction of mammal populations in Western North American national parks. Conserv. Biol. 9:512-526.

Nicolaus L. K. 1987. Conditioned aversions in a guild of egg predators: implications for aposematism and prey defense mimicry. Am. Midl. Nat. 117:405-419.

Nicolaus L. K., P. V. Farmer, C. R. Gustavson and J. C. Gustavson 1989a. The potential of estrogen-based conditioned aversion in controlling depredation: a step closer toward the "magic bullet". Appl. Anim. Behav. Sci. 23:1-14.

Nicolaus L. K., J. Herrera, J. C. Nicolaus and C. R. Gustavson 1989b. Ethinyl estradiol and generalized aversions to eggs among free-ranging predators. Appl. Anim. Behav. Sci. 24:313-324.

Nicolaus L. K., T. E. Hoffman and C. R. Gustavson 1982. Taste aversion conditioning in free Raccoons (*Procyon lotor*). Northwest Science 56:165-169.

Niemuth N. D. and M. S. Boyce 1995. Spatial and temporal patterns of predation of simulated sage grouse nests at high and low densities: an experimental design. Can. J. Zool. 73:819-825.

Obbard M. E. and R. J. Brooks 1980. Nesting migrations of the snapping turtle (*Chelydra serpentina*). Herpetologica 36:158-162.

Österholm H. 1966. The significance of distance receptors in the feeding behaviour of the fox, *Vulpes vulpes* L. Acta Zool. Fennica 106:1-31.

Ough W. D. 1979. Influence of probability and magnitude of reward upon raccoon foraging behavior. M.Sc. Thesis, Nebraska University, Lincoln. 138pp.

Packard G. C., G. L. Paukstis, T. J. Boardman and W. H. N. Gutzke 1985. Daily and seasonal variation in hydric conditions and temperature inside nests of common snapping turtles (*Chelydra serpentina*). Can. J. Zool. 63:2422-2429.

Pasitschniak-Arts M. and F. Messier 1995. Predator identification at simulated waterfowl nests using inconspicuous hair catchers and wax-filled eggs. Can. J. Zool. 73:984-990.

Patterson R. 1971. The role of urination in egg predation defense in the desert tortoise (*Gopherus agassizi*). Herpetologica 27:197-199.

Peterson E. A., W. C. Heaton and S. D. Wruble 1969. Levels of auditory response in fissipeds carnivores. J. Mammal. 50:567-578.

Petokas P. J. and M. M. Alexander 1980. The nesting of *Chelydra serpentina* in Northern New-York. J. Herpetol. 14:239-244.

Pilleri G. 1960. Das Gehirn von *Mustela vison* und *Mephitis mephitis* (Carnivora, Mustelidae). Rev. Suisse Zool. 67:141-158.

Pimm S. L. and J. L. Gittleman 1992. Biological diversity: Where is it ?. Science 255:940.

Pubols L. M., B. H. Pubols Jr. and B. L. Munger 1971. Functional properties of mechanoreceptors in glabrous skin of the raccoon forepaw. Exp. Neurol. 31:165-182.

Pubols B. H. Jr., W. I. Welker and J. I. Johnson Jr. 1965. Somatic sensory representation of forelimb in dorsal root fibers of raccoon, coatimundi, and cat. J. Neurophysiol. 28:312-341.

Pyke G.H. 1978. Are animals efficient harvesters ? Anim. Behav. 26:241-250.

Rasmusson D. D. and B. G. Turnbull 1986. Sensory innervation of the raccoon forepaw: 2. Response properties and classification of slowly adapting fibers. Somatosensory Res. 4:63-75.

Ray H. and G. S. Doetsch 1990. Coding of stimulus location and intensity in populations of mechanosensitive nerve fibers of the raccoon: I. Single fiber response properties. Brain Res. Bull. 25:517-532.

Rensh Von B. and G. Dücker 1963. Haptisches Lern. und unterschei- dungsvermogen bei einem Waschbären. Z. Tierpsychol. 20:608-615.

Ricard L. 1986. Etude éthologique du raton laveur (*Procyon lotor*). Ph.D. Thesis, Université de Montréal, Montréal. 269pp.

Riopelle A. J. 1953. Transfer suppression and learning sets. J. Comp. Physiol. Psychol. 37:108-114.

Rivest P. and J. M. Bergeron 1981. Density, food habits, and economic importance of raccoons (*Procyon lotor*) in Québec agrosystem. Can. J. Zool. 59:1755-1762.

Robinson C. and R. J. Bider 1988. A strategy to decrease predation of snappping turtle (*Chelydra serpentina*) nests. J. Herpetol. 22:470-473.

Roy L. D. and M. J. Dorrance 1992. Efficacy and selectivity of eggs and tallow baits for skunk control. Wildl. Soc. Bull. 20:326-330.

Sanderson G. C. 1987. Raccoon. *In* Wild Furbearer Management and Conservation in North America. *Edited by* Novak M., J. A. Baker, M. E. Obbard, and B. Malloch. Ontario Ministry of Natural Resources. pp. 487-499.

Sargeant A. B., S. H. Allen and R. T. Eberhardt 1984. Red fox predation on breeding ducks in midcontinent North America. Wildl. Monogr. 89:1-41.

Schneider D. G., D. Mech and J. Tester 1971. Movements of female raccoons and their young as determined by radio-tracking. Anim. Behav. Monogr. 4:1-43.

Schoonover L. J. and W. H. Marshall. Food habits of the raccoon (*Procyon lotor*) in North-Central Minnesota. J. Mammal. 32:422-428.

Schowalter D. B. and J. R. Gunson 1982. Parameters of population and seasonal activity of striped skunks, *Mephitis mephitis*, in Alberta and Saskatchewan. Can. Field-Nat. 96:409-420.

Schwartz C. W. and E. R. Schwartz 1974. The three-toed box turtle in Central Missouri: Its population, home range, and movements. Missouri Departmebnt of conservation, Terrestrial Series 5:1-28.

Schwarzkopf L. and R. J. Brooks 1987. Nest-site and offspring sex ratio in painted turtles, *Chrysemis picta*. Copeia 1987:53-61.

Semel B. and L. K. Nicolaus 1992. Estrogen-based aversion to eggs among free-ranging raccoons. Ecol. Applic. 2:439-449.

Shell W. F. and A. J. Riopelle 1957. Multiple discrimination learning in raccoons. J. Comp. Physiol. Psychol. 50:585-587.

Shirer H. W. and H. S. Fitch 1970. Comparison from radio-tracking of movements and denning habits of the raccoon, striped skunk and opossum in Northeastern Kansas. J. Mammal. 51:491-503.

Siegel S. and N. J. Castellan Jr. (eds.) 1988. Nonparametric statistics for the behavioral sciences.(2nd ed). McGraw-Hill, New-York. 399pp.

Sinclair A. R. E., D. S. Hik, O. J. Schmitz, G. G. E. Scudder, D. H. Turpin, and N. C. Larter 1995. Biodiversity and the need for habitat renewal. Ecological Applications 5:579-587.

Snow J. E. 1982. Predation on painted turtle nest: nest survival as a function of nest age. Can. J. Zool. 60:3290-3292.

Sonenshine D. E. and E. L. Winslow 1972. Contrasts in distribution of raccoons in two Virginia localities. J. Wild. Manage. 36:838-847.

Stancyk S. E. 1982. Non-human predators of sea turtles and their control. *In* Biology and conservation of sea turtles. *Edited by* K.A. Bjorndal. Smithsonian Institution Press, Washington, D.C. pp.139-152.

Stancyk S. E., O. R. Talbert and J. M. Dean 1980. Nesting activity of the loggerhead turtle *Caretta caretta* in South Carolina II. Protection of nests from raccoon predation by transplantation. Biol. Conserv. 18: 289-298.

Stegeman L. C. 1937. Notes on young skunks in captivity. J. Mammal. 18:194-202.

Stoddart D. M. (ed.) 1980. The ecology of vertebrate olfaction. Chapman and Hall, London, New-York. 234pp.

Storm G. L. 1972. Daytime retreats and movement patterns of skunks on farmlands in Illinois. J. Wildl. Manage. 36:32-45.

Strong P. N. and M. Hedges 1966. Comparative studies in simple od-dity learning. I Cats, raccoons, monkeys and chimpanzees. Psychon. Sci. 5:13-14.

Stuewer F. W. 1943. Raccoons: their habits and management in Michigan. Ecol. Monogr. 13:203-257.

Talbert R. O. Jr., S. E. Stancyk. J. M. Dean and J. M. Will 1980. Nesting activity of the loggerhead turtle (*Caretta caretta*) in South Carolina I: A rookery in transition. Copeia 1980:709-718.

Taulman J. F. and J. H. Williamson 1994. Food preferences of captive wild raccoons, *Procyon lotor*, from East Texas. Can. Field-Nat. 108:170-175.

Temple S. A. 1987. Predation on turtle nests increases near ecological edges. Copeia 1987:250-252.

Tevis L. Jr. 1947. Summer activities of California raccoons. J. Mammal. 28:323-332.

Thackray R. I. and K. M. Michels 1958. Externally-aroused drives in the raccoon. Anim. Behav. 6:3-4.

Tinkle W. D., D. J. Congdon and P. C. Rosen 1981. Nesting frequency and success: Implications for painted turtle. Ecology 62:1426-1432.

Traversy N., R. McNicoll et R. Lemieux 1989. Les populations de ratons laveurs du sud-ouest du Québec. Québ., Min. Loisir, Chasse et Pêche, Dir. gestion des espèces et des habitats. 114pp.

Tuberville T. D. and V. J. Burke 1994. Do flag markers attract turtle nest predators ? J. Herpetol. 28:514-516.

Turnbull B. G. and D. D. Rasmusson 1986. Sensory innervation of the raccoon forepaw: 1. Receptor types in glabrous and hairy skin and deep tissue. Somatosensory Res. 4:44-62.

Urban D. 1970. Raccoon populations movement patterns and predation on a managed waterfowl marsh. J. Wildl. Manage. 34:372-382.

Verts B. J. (ed.) 1967. The Biology of the Striped Skunk. University of Illinois Press. Chicago. 218pp.

Wade-Smith J. and M. E. Richmond 1982. Reproduction in captive striped skunks (Mephitis mephitis). Am. Midl. Nat. 100:452-455.

Wade-Smith J. and B. J. Verts 1982. Mephitis mephitis. Am. Soc. Mammal. (Pub.). Mammalian species 173:1-7.

Warren J. M. and H. B. Warren 1962. Reversal learning by horse and raccoon. J. Genet. Psychol. 100:215-220.

Welker W. I. and G. B. Campos 1963. Physiological significance of sulci in somatic sensory cerebral cortex in mammals of the family procyonidae. J. Comp. Neurol. 120:19-36.

Welker W. I., J. I. Johnson Jr. and B. H. Pubols Jr. 1964. Some mor-phological and physiological characteristics of the somatic sensory system in raccoons. Am. Zool. 4:75-94.

Welker W. I. and S. Seidenstein 1959. Somatic and sensory representation in the cerebral cortex of the raccoon (*Procyon lotor*). J. Comp. Neurol. 111:469-501.

Wells M. C. 1978. Coyote senses in predation: environmental influences on their relative use. Behavioural Processes 3:149-158.

Wells W. I and P. N. Lehner 1978. The relative importance of the distance senses in coyote predatory behaviour. Anim. Behav. 26:251-258.

Whitney L. F. 1933. The raccoon- Some mental attributes. J. Mammal. 14:108-114.

Wilhoft D. C., M. G. Del Baglivo and M. D. Del Baglivo 1979. Observations on mammalian predation of snapping turtles nests. J. Herpetol. 13:435-438.

Wilkinson L. 1989. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, ILL..

Wilson E. O. and F. M. Peter (eds.) 1988. Biodiversity. National Academy Press, Washington D.C. 521pp.

Wollack C. H. 1965. Auditory thresholds in the raccoon (*Procyon lotor*). J. Audit. Res. 5:139-144.

Yeager L. E. and W. H. Elder 1945. Pre and post-hunting season foods of raccoons on an Illinois goose refuge. J. Wild. Manage. 9:48-56.

Yeager L. E. and R. G. Rennels 1943. Fur yield and autumn foods of the raccoons on Illinois River bottom lands. J. Wildl. Manage. 7:45-60.

Zollman P. E. and R. K. Winkelmann 1962. The sensory innervation of the common North American Raccoon (*Procyon lotor*). J. Comp. Neurol. 119:149-157.

Zolman J. F. 1982. Ontogeny of learning. *In* Perspectives in ethology 5: Ontogeny. *Edited by* Bateson P. P. G. and P. H. Klopfer. Plenum Press, London. pp. 275-323.

APPENDIXES

Appendix 1. Individual performances (number of trials to 80 % success rate) of adult raccoons in 1991 and 1992 in the different tests: Pre-test (PRE); Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). With subject number and sex (male M or female F).

	SUBJECT	SEX	PRE	CONT	TEXT	OLF	COMP
1991	R1	F	80	-	-	-	-
	R2	M	65	75	120	30	-
	R3	F	139	30	100	30	-
	R4	M	70	40	115	35	-
	R5	M	99	45	90	30	-
	R6	F	55	70	105	25	-
1992	R7	F	36	55	80	35	30
	R8	M	109	30	120	30	35
	R9	M	74	45	130	35	30
	R10	M	82	30	115	30	30
	R11	F	70	-	-	-	-
	R12	F	119	75	140	-	-

Appendix 2. Individual performances (number of trials to 80% success rate) of adult skunks in 1992 in the Pre-test (PRE) and the cue-tests: Contrast-test (CONT); and Olfaction-test (OLF). With subject number and sex (male M of female F).

SUBJECT	SEX	PRE	CONT	OLF
S8	M	130	80	30
S9	M	186	-	-
S10	M	150	155	-
S11	F	226	120	-
S12	F	135	130	-
S13	M	226	65	-

Appendix 3. Individual performances (number of trials to 80% success rate) of adult skunks in 1993 in the Pre-test (PRE) and the cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP). With subject number and sex (male M or female F).

SUBJECT	SEX	PRE	CONT	TEXT	OLF	COMP
S10	M	130	75	140	70	-
S11	F	49	90	140	45	65
S12	F	130	40	115	60	85
S13	M	115	25	110	50	65
S14	M	225	65	-	50	-

Appendix 4.a. Performance ratios of adult raccoons based on performances (number of trials to 80% success rate) in three cue-tests: Contrast-test (CONT); Texture-test (TEXT); and Olfaction-test (OLF).

SUBJECT	CONT	TEXT	OLF
R7	32.35	47.05	20.60
R8	16.66	66.67	16.66
R9	21.44	61.90	16.66
R10	17.14	65.72	17.14

Appendix 4.b. Performance ratios of adult raccoons based on performances (number of trials to 80% success rate) in four cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP).

SUBJECT	CONT	TEXT	OLF	COMP
R7	27.50	40.00	17.50	15.00
R8	13.95	55.82	13.95	16.28
R9	18.75	54.17	14.58	12.50
R10	14.63	56.10	14.63	14.63

Appendix 5.a. Performance ratios of adult skunks (sample SI) based on performances (number of trials to 80% success rate) in three cue-tests: Contrast-test (CONT); Texture-test (TEXT); and Olfaction-test (OLF).

SUBJECT	CONT1	TEXT	OLF
S10	42.46	38.36	19.18
S11	39.35	45.90	14.75
S12	42.62	37.71	19.67
S13	28.89	48.89	22.22

Appendix 5.b. Performance ratios of adult skunks based on performances (number of trials to 80% success rate) in four cue-tests: Contrast-test (CONT); Texture-test (TEXT); Olfaction-test (OLF); and Compaction-test (COMP).

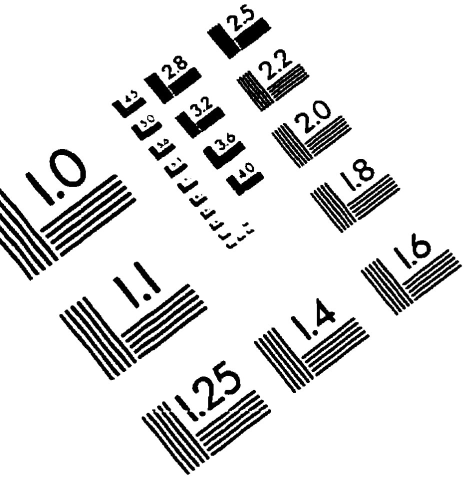
SUBJECT	CONT1	TEXT	OLF	COMP
S11	32.43	37.84	12.16	17.57
S12	33.33	29.49	15.38	21.80
S13	22.41	37.94	17.24	22.41

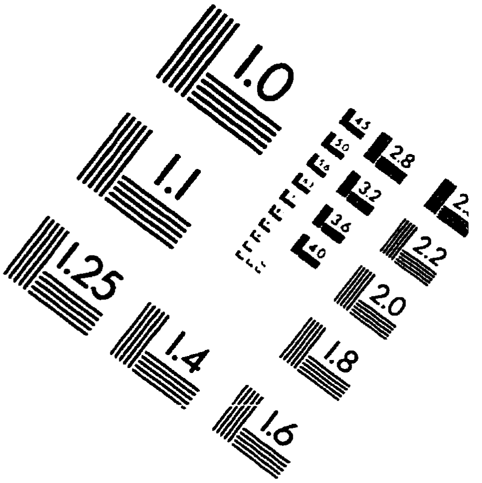
Appendix 6. Performances (number of trials to 80% success rate) of lot 1 and lot 2 juvenile skunks in the Pre-test (PRE) and the different cue-tests: Compaction-test (COMP); Olfaction-test (OLF); Contrast-test (CONT); and Texture-test (TEXT).

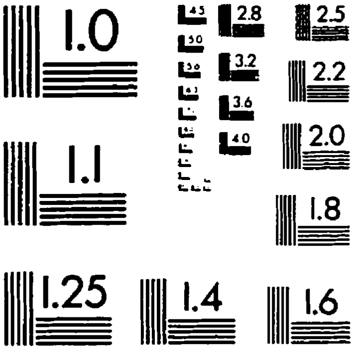
LOT 1	PRE	COMP	OLF	CONT	TEXT
L1	76	65	45	65	110
L3	101	55	30	60	50
P3	126	60	30	30	40

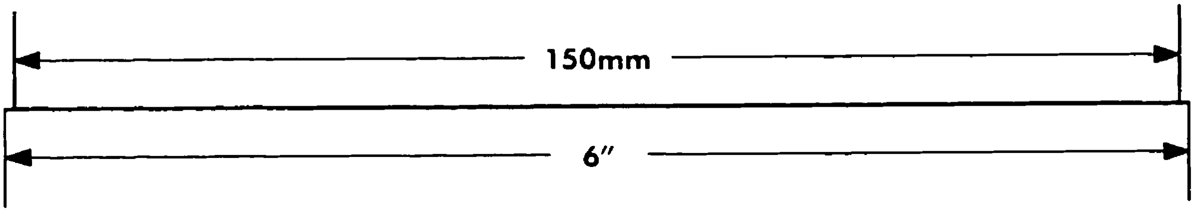
LOT 2	PRE	CONT	OLF	COMP	TEXT
L2	96	40	25	45	40
P1	75	55	60	55	55
P2	93	60	30	65	50

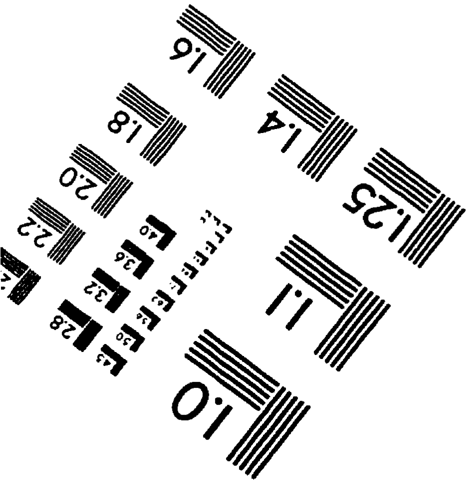
IMAGE EVALUATION
TEST TARGET (QA-3)

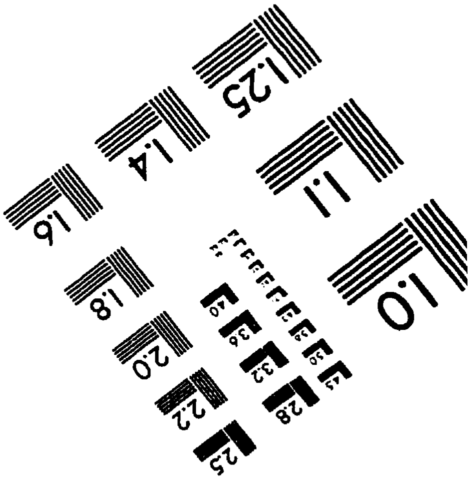












APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved