

BROOD SIZE PREFERENCES OF BROODS OF MALLARD DUCKLINGS (*Anas*
platyrhynchos platyrhynchos)

by

Tyler J. Wereha

A Thesis
Submitted to the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements for the Degree of

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CONTENTS

ACKNOWLEDGEMENTS.....	ii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vi
ABSTRACT.....	viii
INTRODUCTION.....	1
DEVELOPMENTAL CONDITION AT HATCHING.....	5
THE ROLE OF THE ENVIRONMENT ON BEHAVIOUR.....	9
ECOLOGY OF THE MALLARD DUCKLING.....	11
DIFFERENCES AMONG PRECOICIAL AVIAN SPECIES.....	12
RELATIONSHIP BETWEEN MOTHER AND BROOD.....	14
THE BROOD.....	18
CRECHE BEHAVIOUR.....	21
INDIVIDUAL RECOGNITION.....	24
IMPRINTING.....	28
Basic technique.....	31
Early studies into the basic principles of imprinting.....	31
Irreversibility.....	34
Sensitive period.....	35
End of the sensitive period.....	36
CRITICISM OF IMPRINTING.....	37
Inappropriate subjects.....	38
Inappropriate stimuli.....	38
Inappropriate terminology.....	39
Inappropriate rearing methods.....	40
EFFECTS OF SOCIAL EXPERIENCE VS ISOLATION ON PEER RELATIONS.....	40
“PEER IMPRINTING”.....	44
THE PROBLEM WITH “PEER IMPRINTING”.....	52

TESTING THE PREFERENCES OF A BROOD.....	53
Klopfer's (1959) study of the brood.....	53
Methodology for testing the preferences of a brood	54
Results of the methodology.....	56
THE PURPOSE OF THESE EXPERIMENTS.....	56
GENERAL METHODS.....	58
Subjects.....	58
Egg source.....	58
Incubation.....	59
Hatching.....	59
Leg banding.....	60
Rearing conditions.....	60
Experimental subjects.....	61
Stimulus objects.....	62
Randomization of subjects.....	63
Apparatus.....	64
Procedure.....	66
Testing (stimulus objects).....	66
Testing (experimental brood).....	67
Time spent with models.....	68
Number of entries.....	69
Latency.....	69
Behavioural notes.....	69
Statistical analysis.....	69
EXPERIMENT 1: IS AN EXPERIMENTAL BROOD OF 10 DUCKLINGS ATTRACTED TO A SMALLER STIMULUS BROOD OF THREE DUCKLINGS?.....	70
Methods.....	71
Subjects.....	71
Experimental subjects.....	71
Stimulus objects.....	71
Apparatus.....	71
Procedure.....	72
Results.....	72
Discussion.....	80

EXPERIMENT 2: IS AN EXPERIMENTAL BROOD OF 10 DUCKLINGS ATTRACTED TO A SMALLER STIMULUS BROOD OF THREE DUCKLINGS OR A STIMULUS BROOD SIMILAR IN SIZE TO THE EXPERIMENTAL BROOD?.....	81
Hypotheses.....	82
Methods.....	83
Subjects.....	83
Experimental subjects.....	83
Stimulus objects.....	83
Apparatus.....	83
Procedure.....	84
Results.....	84
Discussion.....	91
Duckling behaviour.....	92
The effect of presenting two broods.....	92
The effect of two broods on latency.....	93
The effect of two broods on variability.....	95
Implications of Experiment 2.....	97
EXPERIMENT 3: REPLICATION OF EXPERIMENT 2 USING A LARGER APPARATUS.....	97
Hypotheses.....	98
Methods.....	98
Subjects.....	98
Experimental subjects.....	98
Stimulus objects.....	99
Apparatus.....	99
Procedure.....	101
Results.....	101
Discussion.....	110
EXPERIMENT 4: IS A BROOD ATTRACTED TO A LARGER BROOD?.....	111
Hypotheses.....	112
Methods.....	112
Subjects.....	112
Experimental subjects.....	112
Stimulus objects.....	113
Apparatus.....	114
Procedure.....	114
Results.....	114
Discussion.....	120
GENERAL DISCUSSION.....	122
Behaviour of the stimulus broods.....	127
Distress vocalizations.....	129
Improving the methodology.....	130

Future research.....	132
Why a larger brood?.....	133
REFERENCES.....	136

LIST OF TABLES

TABLE 1: Developmental continuum of hatchlings from altricial to superprecocial.....	8
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LIST OF FIGURES

FIGURE 1: Hypothetical representation of the some factors influencing the formation of attachments in hatchlings with or without a parent present	6
FIGURE 2: Overhead view of the experimental platform.....	65
FIGURE 3: Mean time the experimental broods took to make a choice among quadrants in Experiment 1.....	74
FIGURE 4: Experiment 1: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing the corner cage of the stimulus brood of three ducklings or an empty quadrant.....	77
FIGURE 5: Mean time the experimental broods took to make a choice among quadrants in Experiment 2.....	86
FIGURE 6: Experiment 2: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing the stimulus brood of nine, the stimulus brood of three, and two empty quadrants	89
FIGURE 7: Overhead view of the enlarged experimental platform.....	100
FIGURE 8: Mean time the experimental broods took to make a choice among quadrants in Experiment 3.....	103
FIGURE 9: Mean time the experimental broods took to make a choice among quadrants in Experiments 2 and 3.....	105

FIGURE 10:	Experiment 3: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing the stimulus brood of nine, the stimulus brood of three and three empty quadrants	108
FIGURE 11:	Mean time the experimental broods took to make a choice among quadrants in Experiment 4.....	116
FIGURE 12:	Experiment 4: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing a stimulus brood of three, nine, or 17 ducklings, or an empty quadrant.....	118

Abstract

Most investigations concerning the attachment between a duckling and its mother have used the mallard duckling (*Anas platyrhynchos platyrhynchos*) as their subject. Much of this research examines the attachment in the laboratory. In the natural environment, however, ducklings form attachments to both the mother and to broodmates. When tested individually, there is substantial evidence suggesting that a very strong attachment exists among broodmates (Collias & Collias, 1956; Shapiro, 1980b), that larger broods are preferred, and that attachment to broodmates may be more important than the attachment to the mother (Shapiro, 1980b). In this study, four experiments were conducted to 1) develop a methodology for testing the preferences of an entire brood of ducklings, and 2) to determine the preferences of a brood of 10 ducklings for larger broods. The results of these studies suggest that, like individually tested ducklings, larger broods are preferred. A brood of three ducklings was preferred significantly more than empty quadrants. A brood of nine ducklings was preferred significantly more than a brood of three ducklings or empty quadrants. A brood of 17 ducklings was preferred more than a brood of three or nine ducklings but not to a statistically significant degree. It is suggested that broods of ducklings are attracted to larger broods due to the fitness advantages associated with larger broods.

INTRODUCTION

Survival for many young organisms is dependent upon their forming attachments early in their lives. The attachment between a hatchling and its mother has been extensively studied in precocial avian species (for reviews, see Bateson, 1966; Bolhuis, 1991; Shapiro, 1980b; Sluckin, 1973; Sluckin & Salzen, 1961). Attachment among siblings, however, has not received as much attention. Interest in the hatchling-mother attachment is largely attributed to the work of Konrad Lorenz (1935/1957), who coined the term "imprinting" in reference to the process in which a precocial hatchling comes to follow the first moving object to which it is exposed. Lorenz's (1935/1957) definition is paradoxical because in the natural environment the hatchling is usually simultaneously exposed to both a caregiver and its brood-mates (Gaioni, Hoffman, Klein, & DePaulo, 1977; Shapiro, 1980b). Contrary to what actually happens in the natural environment, the focus of most "imprinting" research has been on the attachment between a duckling and its mother. Much of this research has utilized mallard ducks (*Anas platyrhynchos platyrhynchos*).

"Imprinting" was thought to have certain characteristics that set it apart from other learning processes. Notably, it did not involve any obvious form of reinforcement, it occurred within a distinct period after hatching, and it was irreversible (Lorenz, 1935/1957), leading some to refer to it as "immediate learning" (Jaynes, 1958a).

Despite the attention that "imprinting" has received, the results have been inconsistent (Shapiro & Greenberg, 1974). Some researchers believe that the findings obtained from "imprinting" research may be an artifact of laboratorization (Shapiro & Greenberg, 1974). It has been suggested that the term avian attachment behaviour should

be used instead of the term “imprinting” in recognition of some of the problems associated with “imprinting” research and the fact that other mechanisms may underlie different forms of attachment (Shapiro, 1970). Shapiro (1972a) suggests that the family is not exclusively united by the bond between a duckling and the hen, but is also maintained, in part, by a bond among ducklings. Using the term “imprinting” suggests the existence of the phenomenon, and implies a set of assumptions in the interpretation of avian attachment. Therefore, in this thesis, the existence of “imprinting” will be considered to be tentative and is not an acceptance of the phenomenon, but is used because it is the term used in past research.

Despite the emphasis on the mother in “imprinting” research, many researchers have observed that the brood may also be important to a hatchling. Lorenz (1935/1957) stated that “imprinting is often effected through the influence of parents and siblings” (p.109). Lorenz also observed that, “the parent bird does not form the nucleus of the flock—the offspring primarily congregate with one another and exhibit only secondary attachment to the parents” (Lorenz, 1935/1970, p. 235). Collias and Collias (1956) observed that “the brood shows a strong tendency to stay together, whether or not a parent is present” (p. 391). Nice (1962) stated “little ducklings have a very strong bond to one another—a great need for companionship in their fellows” (p.55). Lickliter and Gottlieb (1986a) state “despite the very large literature on the imprinting process, surprisingly little information is available on the development of social attachments by precocial birds in their natural brood situation” (p. 266).

Many experiments have been conducted examining the attractiveness of peers to a single precocial hatchling. Guiton (1959) noticed that a single chick (*Gallus domesticus*) is more quickly attracted to a group of chicks than to a single chick. Gray (1961) found that a chick would respond less to objects manifesting natural phenotypic colours when another chick was presented to it. Shapiro (1971) found that a live duckling is more attractive to a naïve duckling than an inanimate object. Rogan and Shapiro (1972) found that Peking ducklings (*Anas platyrhynchos*, the domesticated form of mallard) and mallard ducklings (Rogan & Shapiro, 1974) prefer the largest brood available to them. Bruce and Shapiro (1977a) found that ducklings prefer any brood of the same size and of the same species, even if it is not their own. Ducklings also prefer the largest brood available to them, even an abnormally large one (Bruce & Shapiro, 1977a). The brood may even be more attractive to a hatchling than a hen. Shapiro and Bruce (1977) found that a duckling prefers its own brood to its mother or a strange hen, and prefers any hen associated with the largest brood. Storey and Shapiro (1979) found that a brood used as one stimulus object and a hen associated with a maternal call used as another stimulus object are equally attractive to a duckling. Ducklings prefer older broods (Lindren & Shapiro, 1990) and prefer any hen with a brood, regardless of alterations to her natural plumage (Darczewska & Shapiro, 1997). Siblings and peers are also important in other species. In testing individual recognition in Canada geese (*Branta canadensis*), Radesäter (1976) found that a gosling prefers a brood of strange goslings to a single member of its own brood. He also found that a gosling prefers its own brood and a strange brood equally in its first week of life.

A brood is very important to ducklings. It has been suggested that ducklings may prefer a brood for three reasons: warmth provided from other ducklings (Gorman & Milne, 1972), potential anti-predator benefits (Caro, 1986; Hamilton, 1971; Munro & Bedard, 1977, Roberts, 1997), and the facilitation of food accrual (Beard, 1969; McKinney, 1969; Moore, 1977).

Whereas most studies have examined the preferences of a single duckling, Wereha and Shapiro (2005) created a methodology for examining the preferences of an entire brood. They found that a brood of 10 ducklings was attracted to a smaller brood of strange ducklings. Previous experiments testing a single duckling have shown that a single duckling is attractive to another single duckling (Shapiro, 1971) and that a single duckling will prefer the largest brood available to it whether it was reared communally (Rogan & Shapiro, 1973) or in isolation (Rogan & Shapiro, 1972). Wereha and Shapiro (2005) found that a brood of 10 ducklings preferred a brood of three strange ducklings significantly more than empty quadrants. This result raises many interesting questions. Why would a brood of 10 ducklings be attracted to a smaller brood of strange ducklings? If larger broods are preferred (i.e. Rogan & Shapiro, 1974), why would the ducklings in a large group be attracted to a smaller group of ducklings?

The methodology of Wereha and Shapiro's (2005) study provides the basis for a series of experiments in which the preferences of an entire brood of ducklings can be examined. Although the mother is important to a duckling, perhaps her importance has been overemphasized in the traditional "imprinting" literature. A wealth of research has shown that a brood is highly attractive to a single duckling. This study will examine the preferences of an entire brood of mallard ducklings for other broods of various sizes.

DEVELOPMENTAL CONDITION AT HATCHING

Studies in avian attachment behaviour have generally used precocial avian species (Bateson, 1966), especially the mallard duckling (*Anas platyrhynchos platyrhynchos*).

The formation of attachments in hatchlings can be a function of three factors: whether the parent is present, its dependence upon a caregiver, and the quality of the environment in which it is raised (Shapiro, 1980b). If these three factors are thought of as forming the dimensions of a cube (Figure 1), the formation of an attachment in hatchlings can be thought of as the product of an interaction among these three factors. For example, altricial hatchlings, in the bottom left hand corner of the cube, have one or more parents present to care for them. Altricial hatchlings are born relatively underdeveloped. They are psilopaedic and nidicolous, meaning that they are born naked or with very little down, and remain in the nest for an extended period of time after hatching (Skutch, 1976). Altricial hatchlings are highly dependent upon a caregiver to survive since they are born in a less advanced state of development. Altricial bird species include, among others, songbirds, woodpeckers, and parrots.

Progressing up to the top right hand corner of cube, the hatchlings become increasingly developed upon hatching and proportionally less dependent upon the parents. Precocial hatchlings, such as ducklings, are much less dependent upon their parents than altricial organisms. Precocial hatchlings are ptilopaedic and nidifugous (Skutch, 1976), meaning that they are born with a dense covering of down and are able to leave the nest soon after hatching. Since precocial hatchlings are born at a relatively

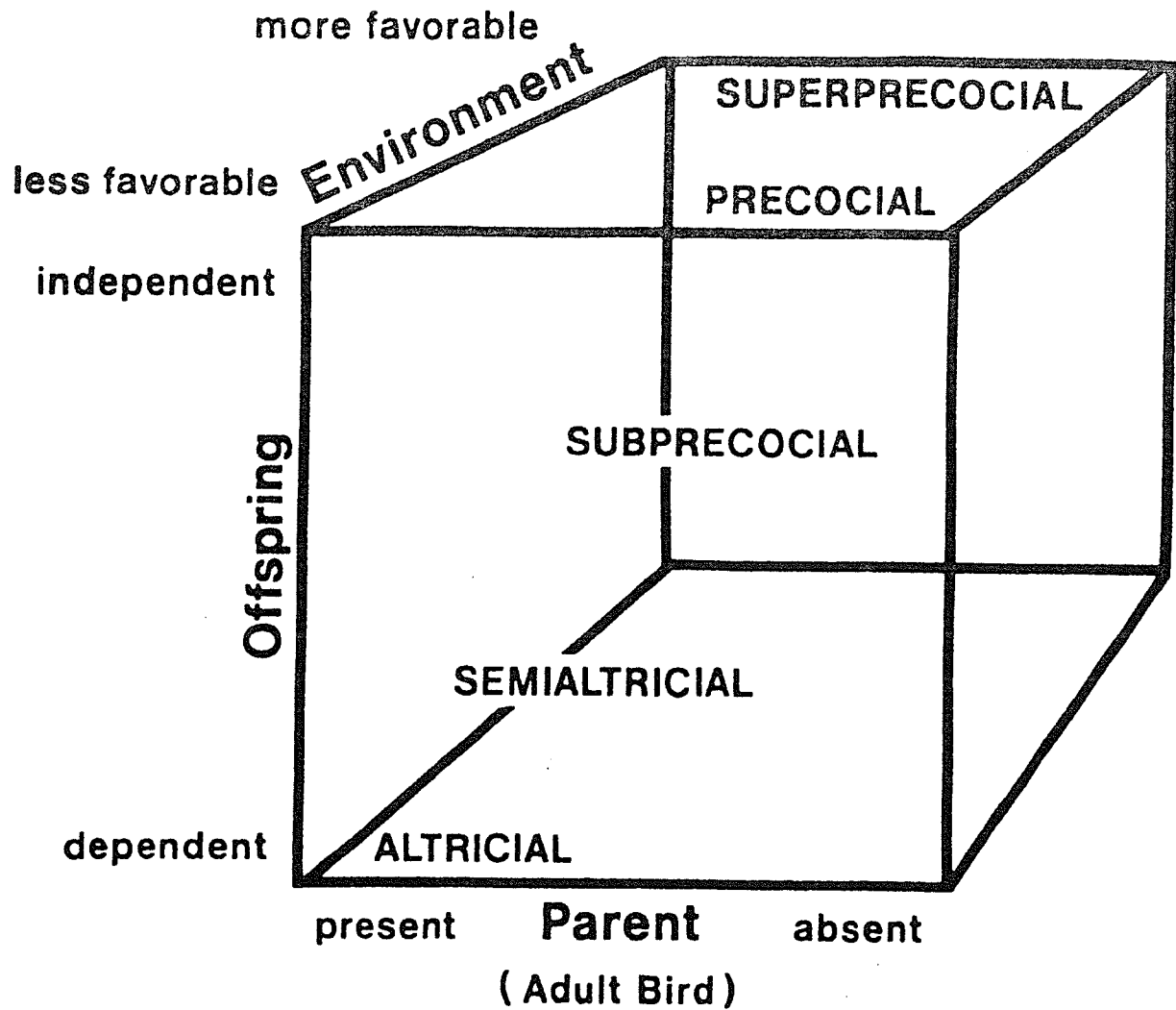


Figure 1. Hypothetical representation of some of the factors influencing the formation of attachments in hatchlings with or without a parent present. Shapiro, L. J. (1980b). Species identification in birds: a review and synthesis. In M. A. Roy (Ed.), *Species Identity and Attachment*, (p. 82). New York: Garland Press.

advanced stage of development and are relatively autonomous, it may be that the parents of precocial hatchlings are less important to them than are parents of altricial hatchlings. It is possible that as the importance of the parents decreases, the importance of a brood to the hatchling increases.

Hatchlings can be categorized based on their condition at hatching (Skutch, 1976). Table 1 shows the developmental continuum under which a hatchling can be classified. Level of development increases from altricial to superprecocial.

The precocial hatchling's ability to locomote has been a major object of study in avian attachment research. Its ability to follow a caregiver has been used as a convenient measure of attachment and is one that cannot be applied to the relatively underdeveloped altricial hatchling. Ducks are considered to be the most precocial of bird species (Nice, 1962), except for the superprecocial megapodes. Megapodes such as the mallee fowl (*Leipoa ocellata*) do not form an attachment with a parent, because none is present when the hatchlings are born. Eggs are laid in a pile of sand and vegetation constructed by the parents. The eggs are incubated by the warmth generated from the decomposition of the vegetation in the pile. The young are born nearly fully developed, and can fly strongly by 24 hr of age (Skutch, 1976).

Why is there a difference in condition at hatching? Would it not be beneficial for all birds to be fully developed at hatching? The answer may be found by looking at the ecology of the organism. Most precocial species have nests that are highly accessible to predators, such as the nests of most ducks, which are on the ground. When precocial birds hatch they are able to follow a parent to safety and escape from predators. The larger egg sizes of precocial birds allow for more nourishment for the developing young and lead to

Table 1

Developmental continuum of hatchlings from altricial to superprecocial

Condition at hatch	1	2	3	4	5	Examples
Superprecocial	yes	yes	yes	no	no	megapodes
Precocial 1	yes	yes	yes	no	yes	ducks, shorebirds
Precocial 2	yes	yes	yes	no	yes	quail, grouse, murrelets
Subprecocial	yes	yes	yes	some	yes	grebes, rails, cranes
Semiprecocial	yes	yes	some	yes	yes	gulls, terns, petrels, penguins
Semialtricial 1	yes	yes	no	yes	yes	hawks, herons
Semialtricial 2	yes	no	no	yes	yes	owls
Altricial	no	no	no	yes	yes	passerines, woodpeckers

Note. Numbers represent the physical state of the hatchling and the presence and influence of parents (1 = *presence of down*, 2 = *eyes open*, 3 = *ambulatory*, 4 = *parents feeding*, 5 = *parents attend [brood, etc.]*). From *Ornithology*, by F. Gill, 1990, p. 378. New York: W. H. Freeman.

well developed hatchlings. This extra nourishment is important for a precocial duckling which is born with an internal three-day supply of yolk (Kear, 1965). This yolk is important to the duckling, as it can utilize this stored energy to follow its mother to safety instead of foraging. Altricial species generally lay their eggs above ground, safe from predators. They lay smaller eggs in comparison, but the young hatch with a much more advanced digestive system than those of precocial hatchlings. Being fed by both parents more than makes up for the lack of nourishment provided by the smaller eggs, leading most altricial species to attain the power of flight before precocial species (Skutch, 1976).

THE ROLE OF THE ENVIRONMENT ON BEHAVIOUR

A problem with much of the imprinting literature is that it has taken what occurs in the natural environment out of context. Experiments that have been conducted on “imprinting” have not taken into account the adaptive significance of forming an attachment in a particular species living in its natural environment with all of the selective pressures that the environment brings to bear upon the organisms involved. For example, learning that a duckling will follow an arbitrarily selected, biologically inappropriate, object such as a green box tells us very little about how this behaviour is adaptive in the natural environment.

Applying the label of “imprinting” to the study of attachment created the connotation that it is a phenomenon, like many others that psychologists study, that can be taken into the laboratory and systematically picked apart. In other words, it downplays the context under which this phenomenon is normally expressed, treating it as a response that is innate to the individual; hence its label as an artifact of the psychologist’s

laboratory (Shapiro & Greenberg, 1974). Shapiro (1980b) suggests that the use of biologically appropriate objects (objects normally encountered in the natural environment) is the only way to obtain meaningful results in the laboratory. Also, even though attachment is an interactive process, many researchers have used inanimate models where live models would have been preferred (Shapiro, 1980b).

The apparent "uniqueness" of the phenomenon has led some researchers to suggest that the phenomenon can be generalized across species. However, generalizations across species should not be made without taking into account the ecology and life history of each species and, more importantly, testing these hypotheses in other species (Breland & Breland, 1966). For example, it has been suggested that altricial bird species may become "imprinted" to parents (Lorenz, 1935/1957). It has even been suggested that "imprinting" may also be applicable to mammals such as guinea pigs (Harper, 1970) and even humans (see Sluckin, 1973). Also, the term "imprinting" has been generalized to phenomena other than attachment (Shapiro, 1980a). For example, snapping turtles (*Chelydra serpentina*) prefer the food that they have been exposed to early in life. This process has been called "food-imprinting" (Burghardt & Hess, 1966). Early experience and "imprinting" have also been linked to preferences much later on in life. For example, Lorenz (1935/1957) suggested that sexual preferences may be established during the "imprinting" period but are not manifested until sexual maturity. It has also been suggested that "imprinting" may play a role in humans as well (Lorenz, 1935/1957).

The study of attachment must take into account the unique behavioural repertoire of an organism. This behavioural repertoire has evolved in response to the demands made upon it by the natural environment in which it lives in order to survive. The study of attachment must begin by studying the ecology of the organism.

ECOLOGY OF THE MALLARD DUCKLING

Before any research on an organism can be conducted in the laboratory, something must be known of its natural environment, as well as how it behaves in its environment (Breland & Breland, 1966). An excellent review of mallard behaviour is provided by McKinney (1969). The following information is adapted from Drilling et al. (2002) unless otherwise stated.

The mallard (*Anas platyrhynchos platyrhynchos*) is the most abundant duck species in North America. It is widely distributed throughout the continent and will winter wherever they have access to open water and to food. Its breeding range extends from the southern United States to Alaska. It nests in a variety of habitats including marshes, farmlands, forests and urban parks. The mallard is a generalist feeder. During the breeding season the mallard's diet consists mainly of insects and other invertebrates. Its diet changes to mostly seeds from natural and agricultural sources outside the breeding season. Urban dwelling populations are reliant upon human-provided foods in the winter. All domesticated ducks, except the domesticated muscovy duck (*Cairina moschata*), are descendants of the mallard (Drilling et al., 2002). The mallard is one of the earliest migrants, arriving during the spring thaw, and is often temporarily driven

back, southward, by freezing weather (Sowls, 1955). The mallard is very gregarious except during a territorial phase at the beginning of the breeding season.

The average clutch size in the mallard is 8 to 12 (Skutch, 1976). Clutch size is determined by nest-initiation date, quality of diet, and condition of the hen, and declines throughout the season (Drilling et al., 2002). One egg is laid each day, with the female spending more time incubating with each egg laid. Only the hen cares for the eggs by incubating and turning them. The hen leaves the nest once or twice a day for a 15-60 min period and spends most of this time feeding. The eggs hatch in 28 days. The ducklings begin vocalizing 2-3 days prior to pipping. These vocalizations function to synchronize hatching (Vince, 1969). As hatching approaches, the hen decreases egg turning and increases her vocalizations. The ducklings hatch within a few hours of each other. Most ducklings leave the nest 13-16 hr after hatching. Though they can become endothermic (i.e. they are able to maintain a relatively constant body temperature) at 24 hr, they require brooding to maintain body temperature until about two weeks of age. Ducklings are highly synchronous in their behaviour. Ducklings spend less time feeding and more time performing comfort and resting activities such as preening as they mature. Mallards are dabbling ducks, meaning that they feed by "tipping up" rather than diving (Drilling et al., 2002).

DIFFERENCES AMONG PRECOCIAL AVIAN SPECIES

Although most avian attachment research has utilized the mallard, other precocial species have also been used (Lorenz, 1935/1957). Despite any similarities among species, one must be careful in generalizing from one species to another. This rule holds true even

among different species of duck. Ducks are a diverse group that have different life histories, exhibit different behaviours, and live in different environments. The family Anatidae is a complex taxonomic group of waterbirds that include true ducks, geese, swans, and whistling-ducks (Elphick, Dunning Jr., & Sibley, 2001).

True ducks belong to the subfamily Anatinae, which is subdivided into several tribes, four of which are found in North America. The mallard belongs to the tribe Anatini, the dabbling or surface-feeding ducks (Elphick et al., 2001). One interesting example that emphasizes the differences across species of duck is that of the obligate brood parasitic black-headed duck (*Heteronetta atricapilla*) of South America. The young of this species are superprecocial. Eggs are hatched in the nests of other ducks. The young rely on their surrogate parents for brooding for two days before leaving to live on their own (Weller, 1968).

Hess and Petrovich (1977) state that many researchers disregard the differences among species despite the “overwhelming evidence from population genetics to make the case that reproductively isolated populations (even those of the same species, or breeds) are often different genetic constellations with different phenotypes” (p. 3). For example, strains of chickens that have been reproductively isolated from one another over many generations may exhibit different behaviours (Hess & Petrovich, 1977). Survival of an organism depends upon the effectiveness and adaptability of its behavioural repertoire to meet the demands of the environment. Differences in the ontogenesis of behaviour, as Hess and Petrovich (1977) put it, is “in part due to their phylogenetic history and in part due to a continuous process of adaptation to specific and different ecological requirements” (p. 4).

Any findings in one species must be tested in another species before any generalizations between them can be made. Indeed, Shapiro (1980b) states that the fact that so few avian species have been studied “precludes any valid generalizations from being made about species identification in birds” (p. 92). The focus of this thesis is on the mallard duck. However, research involving other species will also be reviewed.

Researchers can use information from other species as a foundation from which they can develop hypotheses on their own species of interest. Research involving other species is also a source to look to for evaluating general trends as the same evolutionary forces are at play in different species. Lorenz (1935/1957) stated, “It is essential to study the total behaviour of as many and as closely related species as possible. I predict that such a study will bring into light far better and clearer typological sequences” (p. 100).

RELATIONSHIP BETWEEN MOTHER AND BROOD

The hen serves several functions necessary for her young to survive. Collias (1952) stated, “normally, a broody hen represents to the chick an adaptable complex of attractive stimuli, including warmth, contact, clucking, and movement; and repeated exposure to these stimuli, as well as the food guidance and protection that a hen gives her chicks, helps strengthen the family bond (p. 139).”

The adaptive significance of a duckling to quickly learn to follow its mother is obvious. How the duckling learns to do this has been the foundation of decades of research on the phenomenon known as “imprinting”. This research, however, may have overemphasized the role of the mother. The importance of siblings and peers has been examined only after many years of research focusing on the role of the mother (Dyer,

Lickliter, & Gottlieb, 1989; Johnston & Gottlieb, 1985a; Lickliter & Gottlieb, 1985; Storey & Shapiro, 1979; Wereha & Shapiro, 2003, 2005) and calls into question the use of the mother as the main object of a hatchling's attachment. One may question whether the mother is as important to the ducklings in the natural environment as the imprinting literature implies.

Most "imprinting" research examined the attachment of a duckling to an object in its first two or three days of life. The way in which attachments change over time, however, has not been studied since very few longitudinal studies of avian attachment have been conducted. Attachment is a complex relationship in which the organisms involved exhibit behaviours that foster attachment and change over time. Beard (1964) observed that the strength of the bond between hen and brood is determined by the hen's stage in the reproductive cycle and by the age of the ducklings. Thus, the strongest bond between the brood and hen exists when the brood is very young. Beard (1964) observed that as the brood matures, the hen no longer maintains her almost constant calling to the ducklings, nor does she attempt to maintain the ducklings in a tightly bunched brood formation. By five weeks of age, ducklings become increasingly independent of the female. The time that the brood starts to fly (seven to eight weeks of age) marks the end of the brood-hen bond (Beard, 1964).

As stated earlier, the hen is important to the survival of her young, but how important is debatable. Parental behaviours that can potentially affect duckling survival include incubation, vigilance and other anti-predator behaviours, and brooding (Dzus & Clark, 1997). Researchers such as Dzus and Clark (1997) feel that if the hen is important to the survival of her young, she will only be able to invest her energy in an optimum

number of ducklings. Other researchers have taken the stance that post-hatch parental behaviours in precocial bird species, as opposed to altricial bird species, have little effect on offspring survival. This latter position is supported by the fact that ducklings find their own food and are quite independent shortly after hatching. One can then postulate that increases in brood sizes (post-hatch increases) should not negatively affect the female because the ducklings' survival is not limited by the capacities of the mother.

Many researchers have found that it appears, in fact, that a minimal increase in parental expenditure is required on the part of the precocial female with larger broods (Geffen & Yom-Tov, 2001). Rohwer (1985) found that female blue-winged teal (*Anas discors*) could incubate far more eggs than normal and rear the ducklings without any adverse affect. The same result has been found with wood ducks (*Aix sponsa*) (Rohwer & Heusmann, 1991). Dzus and Clark (1997) found that the proportion of time spent brooding by female mallards did not increase with increases in brood sizes.

Further, the mother may play an important role for only a short time. Ducklings require brooding up to two weeks of age (Drilling et al., 2002). Survey estimates have shown that there is little change in duckling survival after 30 days of age (Rotella & Ratti, 1992). Ducklings hatch with the thickest and most complete down plumage of any species except the megapodes and require little warming (Nice, 1962). Ducklings are not exclusively dependent upon the mother for thermoregulation either (Gorman & Milne, 1972). Ducklings spend most of their time huddling together (Hicinbothom & Miller, 1999; Levy & Shapiro, 2004; Wereha & Shapiro, 2005). Chicks also spend most of their time together and seldom stray from the group (Guiton, 1959).

Other researchers, however, believe that post-hatch parental care is important to duckling survival. Dzus and Clark (1997) postulate that duckling survival could be reduced by the female's inability to effectively cover a brood. They found that mallard ducklings in enlarged groups had lower rates of survival than controls. Both enlarged and control broods, however, had a higher survival rate than the reduced broods. Arnold, Rohwer, and Armstrong (1987), in a review of Rohwer's work, found a decrease in hatchability and increased incubation times in enlarged clutches. Clutches and post-hatch survival are two different situations, however, each governed by a different set of environmental parameters.

Brood size is also often determined by factors other than the mother's ability to incubate a large clutch. Environmental conditions such as habitat conditions (Ball, Artmann, & Hoekman, 2002; Krapu, Pietz, Brandt, & Cox, 2000; Rohwer, 1985; Rotella & Ratti, 1992; Toft, Trauger, & Murdy, 1984), wetland density (Dzus & Clark, 1998), and weather (Lessells, 1986; Krapu et al., 2000) have a large affect on brood size. Time of the season is another factor. Brood sizes decrease as the season progresses (Dzus & Clark, 1998; Krapu et al., 2000; Rotella & Ratti, 1992; Toft, Trauger, & Murdy, 1984), and the survival of these later broods is often lower (Dzus & Clark, 1998; Krapu et al. 2000). Seasonal decline in brood sizes is perhaps the most pervasive and consistent reproductive pattern in birds (Klomp, 1970).

These studies indicate that survival of ducklings is often a function of factors other than the mother's ability to care for her brood. With this being the case, is an attachment to the mother necessary for the survival of a duckling? In other words, is the emphasis of the mother in the "imprinting" literature warranted given the relative

autonomy of the precocial duckling? Shapiro and Bruce (1977) have shown that when given a choice between their own mother, a strange mother, and a strange brood, mallard ducklings prefer the brood. In fact, when mallard ducklings are given a choice between a hen with a brood and a hen with no brood, they choose the hen with the brood, suggesting that it is the brood that is attractive (Bruce & Shapiro, 1977b). Other researchers contend that continued exposure of the duckling to the mother might be required to maintain a bond between the ducklings and the mother (Johnston & Gottlieb, 1985b). Despite the fact that the duckling is simultaneously exposed to both its mother and its siblings at hatching, the role of siblings has inexplicably been ignored in "imprinting" research.

THE BROOD

Despite some early observations (Collias & Collias, 1956; Lorenz, 1935/1957, Spalding, 1873) regarding the importance of siblings and peers, the role of the brood has been traditionally ignored. Even Lorenz (1935/1957), whose work spawned a great interest in the role of the mother, noted the attachment among hatchlings. Lorenz's mentor, Oscar Heinroth, (as cited in Lorenz, 1935/1957, p. 103) described the behaviour of incubator hatched mallard ducklings. Heinroth stated, "if there are several birds, their need for society is amply satisfied; they hardly miss the leading mother, nor do they attach themselves to human beings" (as cited in Lorenz, 1935/1957, p. 103). Despite these early observations, the role of the mother became the focus of "imprinting" studies.

The importance of the brood to a duckling is readily observed in the natural environment and has been explored in the laboratory. Collias and Collias (1956) have found that the brood is a very cohesive group and will stay together whether or not the

hen is present (p. 391) and that a duckling separated from its brood exhibits distress calls that cease soon after being reunited with its brood (p. 391), a behaviour that is also found in domestic chicks (Guiton, 1959; Kaufman & Hinde, 1961). Collias and Collias (1956) also observed that the young did not immediately follow the female when she left the nest, even when she calls them (p. 383). In an experiment, Collias and Collias (1956) found that a duckling will follow two other ducklings which were trained to follow humans, even though that duckling is not trained to follow humans itself (p. 391). This finding suggests that other ducklings are attractive to a single duckling.

A brood becomes a very exclusive social circle in just a short period of time. Ducklings in a brood readily attack strange ducklings at only a few days of age (Raitasuo, 1964) and display a high degree of synchronization of behaviour (Klopfer & Gottlieb, 1962; Sowls, 1955). Aggression between members of a brood is rare during the first few days after hatching, which may facilitate the social bond (Collias & Collias, 1956). The brood is kept together, in part, by means of "contentment notes" which serve as a means of maintaining contact among ducklings. Contentment notes are more attractive to the ducklings than distress notes (Collias & Collias, 1956). Gaioni (1982), using Peking ducklings, and Gaioni and Platte (1982) using mallard ducklings, however, found that ducklings are sensitive to distress calls as evidenced by their tendency to alternate their distress calls with one another. Other researchers such as Hicinbothom and Miller (1999) state that neither siblings nor the hen respond consistently to the responses of distress vocalizations. Wereha and Shapiro (2005) observed that experimental broods were attracted to the distress vocalizations of ducklings used as stimulus objects when the experimental broods themselves were distress vocalizing.

Ducklings seem to express behavioural changes when the size of their brood is changed. Raitasuo (1964) observed that the behaviour of the brood changes as its size is reduced by predators, with the brood becoming restless if its numbers are reduced below a certain level. Lorenz (1935/1970) stated that although ducklings can recognize each other, distress due to brood size reduction is due to the actual change in numbers, and not due to the absence of any particular brood members (p. 241-242). Gaioni et al. (1977) found distress vocalizations in a brood are proportional to the size of the brood reduction. Gaioni et al. (1977) examined the dynamics of the brood and found that; a) the more a brood is reduced in numbers, the more the remaining ducklings distress vocalize, b) larger broods distress vocalize more than smaller broods in response to brood size reductions, c) neither increasing brood size nor interchanging ducklings between broods induced distress vocalizations, and, d) ducklings changed from a larger brood to a smaller brood or from a smaller brood to a larger brood readily adapted to the new brood size. Raitasuo (1964) stated that ducklings become restless when the size of their brood is reduced. The behaviour of the hen, on the other hand, appears to change little when her brood is reduced in number. In fact, Raitasuo (1964) states that the hen "seems in no way to miss the lost ducklings" (p. 57), although this is disputed by Beard (1964). Lorenz (1935/1970) stated that the mother duck is insensitive to reductions in her brood unless her brood distress vocalizes.

It appears that in the absence of the mother, any brood may be attractive to a single duckling (Raitasuo, 1964). Broods in the natural environment may be kept separated from other broods, in part, by the mother reinforcing her ducklings' aggressive behaviour towards other broods (Collias & Collias, 1956). Ducklings that are separated

from their mother and brood are not aggressive towards strange broods and, in fact, attempt to join them (Raitasuo, 1964). In crowded populations, drakes are known to attack hens with newly hatched ducklings. During these attacks, ducklings may scatter and lose their mothers and join other broods (Drilling et al., 2002). Savard (1987) found that some female Barrow's Goldeneye (*Bucephala islandica*) leave their young of 5 or 6 weeks of age to molt. At this time, the young form large groups, which is "facilitated by the absence of females and the mutual attraction of the young" (p. 1550). Nice (1962) stated that attachment between brood members must often outlast the parental bond. This is especially the case in diving ducks, since these mothers often desert their young before they can fly. Bruce and Shapiro (1977a) have demonstrated that ducklings do not prefer their own brood to another strange brood. A duckling may have a better chance of survival if it joins a brood than it would have on its own (Gorman & Milne, 1972). As stated previously, broods provide warmth, protection from predators, and may assist in finding food.

CRÈCHE BEHAVIOUR

In most bird species, broods generally remain together but are kept separate from other broods. During this time, ducklings are attended to exclusively by their own parent or parents. However, the broods of many species of birds, including several species of waterfowl, amalgamate into large groups called crèches. Many hypotheses have been put forth to explain this phenomenon and much debate exists as to its causes and whether or not it is adaptive. Despite all the controversy as to the exact nature of brood

amalgamation, one underlying commonality in these studies is the mutual attraction of ducklings to one another.

Gorman and Milne (1972) studied crèche behaviour in a breeding population of common eiders (*Somateria mollissima*). Shortly after hatching, the hens led the ducklings to sheltered mudflats on an estuary where broods amalgamated to form crèches of about 500 ducklings. No attempt was made by the hens to select certain ducklings, nor was any aggressive behaviour observed toward any ducklings. The hens, after an average of about four days with the crèche, would leave the crèche, resulting in a constant turnover of hens guarding the crèche. After incubating and brooding, the hens were extremely emaciated and needed to feed, requiring the mothers to leave in order to feed in another area where food was more conducive to the adult diet (Gorman & Milne, 1972).

With no mother, forming a crèche has advantages for a duckling. The ducklings of a crèche provide each other with heat, replacing the brooding behaviour of the hen. A tightly packed group of ducklings allows for a smaller perimeter for the few adults to patrol and protect and may lower the chance of aerial predation by virtue of safety in numbers. It is important to note the effect of the ecology on behaviour. In cases where feeding grounds are conducive to both brood and hen feeding, hens need not abandon their young and crèches are not formed (Gorman & Milne, 1972).

Why does crèching behaviour exist? Gorman and Milne (1972) assume that crèche behaviour is selected for the benefits of the young and the adults. Other researchers, such as Munro and Bedard (1977), believe that there is no cooperation among females and that a marked hierarchy exists among the females tending a crèche. Savard (1987) states that brood amalgamation in Barrow's Goldeneye (*Bucephala*

islandica) and Bufflehead (*Bucephala albeola*) is not adaptive but is rather an accidental outcome of female territorial aggression. Eadie and Lyon (1998) suggest that brood amalgamation is the result of two separate processes: brood desertion and brood adoption. Studying Barrow's goldeneye, Eadie and Lyon (1998) found that a desertion threshold existed below which a female deserts her brood because it is no longer profitable to invest in them. They also found no evidence that crèche formation is driven by the benefits to the ducklings, since ducklings in the crèche did not survive better in larger broods. Gorman and Milne (1972) found that ducklings in crèches did not have as high a survival rate as ducklings that remain with the mother but had a higher survival rate than ducklings that do not join a crèche. Females that accepted orphans had similarly sized young ducklings, whereas older ducklings were met with aggression. The ducklings may be strongly attracted to each other, especially since their own mothers may desert them, and potential host females may attempt to kill them (Eadie & Lyon, 1998). Eadie and Lyon (1998) postulate that because adoption does not appear to be costly to the ducklings, the ducklings may have an interest in maintaining a large brood size.

Debate still exists as to why crèching exists. Alison (1976) states that although communal brooding is presumably of selective advantage in the Oldsquaw (*Clangula hyemalis*), the mechanism enhancing survival of the young is unknown. Eadie, Kehoe, and Nudds (1988) reviewed the hypothesis of brood amalgamation, including hypotheses regarding pre-hatch brood amalgamation by nest parasitism (the laying of eggs of one species in the nest of another species), and post-hatch brood amalgamation by crèching. They found that the majority of the hypotheses put forward have never been tested. The causes applied to brood amalgamation such as parasitism, crèching, and kidnapping,

imply an adaptive basis that may not be justified. They suggest that these different tactics can simply be viewed as part of the same general strategy of brood amalgamation. They also suggest that different hypotheses regarding crèching may apply not only to different species, but to different individuals within each species as well. The general attraction of ducklings to conspecifics seems to be supported by crèching in ducks.

INDIVIDUAL RECOGNITION

Many sibling recognition studies have been conducted in species ranging from single-celled organisms to humans (Fletcher & Michener, 1987; Hepper, 1991). In terms of avian species, many studies of sibling recognition have been conducted on seabirds (Evans, 1970; Palestis & Burger, 1999; Pierotti, Brunton, & Murphy, 1988). Recognition discrimination between parent and offspring is well developed at an early age in colonial species with high nesting densities, in which parents and offspring must be able to recognize each other for feeding and care-giving purposes, and in which the young leave the nest early and form flocks with others of their species (Evans, 1970). Under conditions such as these, where intermingling of young is common, visual and vocal recognition of siblings would be beneficial in maintaining contact in a brood and between the brood and parents. The cohesiveness of the brood may ensure each chick's proximity to the nest and, in conjunction with the enhanced vocal stimulation, stimulate the parents to provide protection and adequate food (Burger, Gochfeld, & Boarman, 1988).

Pierotti, Brunton, and Murphy (1988) tested sibling recognition in western gull chicks (*Larus occidentalis*) by testing the preferences of chicks for familiar siblings, unfamiliar siblings, familiar non-siblings, and unfamiliar non-siblings. The chicks

preferred the familiar individuals regardless of relatedness. Aggression between unfamiliar chicks was rare. It was witnessed on only a few occasions. Common tern chicks (*Sterna hirundo*) prefer broodmates (siblings) to familiar non-siblings (chicks from neighbouring broods) (Palestis & Burger, 1999). They found that learning the identity of siblings is not enough to instill a preference when tested for a choice between siblings and familiar non-siblings. Chicks must learn the identity of both the siblings and the neighbouring chicks in order to discriminate between them (Palestis & Burger, 1999).

Ramsey (1951) provided evidence for individual recognition in several domestic species of birds and found that both adults and young recognize individuals by using colour, voice, size, and form as cues. Ramsey (1951) stated that auditory cues may be the most important cue in recognition. For example, he found that muscovy ducklings, removed from their mother a few hours after hatching, could recognize their mother's vocalizations four days later. Chicks living in groups without a hen can recognize individuals by three days of age (Guiton, 1958, as cited in Guiton, 1959; Vallortigara & Andrew, 1994).

Sigman, Lovern, and Schulman (1978) examined the preferences of chicks for conspecifics reared under various conditions. In the first experiment, white leghorn chicks were reared in two pairs of two chicks each. At 48 hr of age, the chicks reared in pairs were divided; one chick served as the experimental subject and the other chick served as the stimulus object. The experimental subject was placed in a simultaneous choice situation in which the stimulus objects were its familiar broodmate or an unfamiliar socially-reared chick. They found that there was no statistically significant difference in the amount of time a socially-reared chick spent with a familiar socially-

reared chick or an unfamiliar but socially-reared chick. To determine if the lack of any preference for the familiar chick was due to the manner in which the stimulus objects were raised, i.e. socially, the experiment was repeated using an unfamiliar socially-reared chick as one stimulus object and an unfamiliar chick which was reared in isolation as the other stimulus object. The experimental chicks that were reared socially in pairs significantly preferred the unfamiliar socially-reared chicks used as stimulus objects. When chicks reared in isolation were used as the experimental subjects and unfamiliar socially-reared chicks and unfamiliar chicks raised in isolation were used as the stimulus objects, the experimental subjects that were reared in isolation significantly preferred the chicks that were reared socially to the chicks that were reared in isolation. The results of this experiment suggest that chicks can discriminate behavioural differences between conspecifics, preferring those that have been reared socially to those reared in isolation, regardless of whether or not the conspecific was familiar or a stranger (Sigman et al., 1978). The experimenters state that by 48 hr of age, behavioural features, such as the vocalizations, the posturing, and the rate of investigative pecking by the stimulus objects, may be more important than morphological features of individuals in determining approach and stay near preferences in chicks.

Common eider ducklings (*Somateria mollissima*) can recognize and choose to follow a particular female by 27 hr of age (Munro & Bedard, 1977). Even though ducklings can recognize one another individually (Lorenz, 1935/1970), Gaioni et al. (1977) found that interchanging nine-day old mallard ducklings between broods did not induce aggressive behaviour or distress vocalizations from the ducklings. Munro and Bedard (1977) noted that two motherless groups of eight and nine week old ducklings

preserved great stability. Despite many encounters, the groups of ducklings maintained their original compositions.

Another possible mechanism of learning to identify conspecifics is through self-referent phenotype matching, also known as the “armpit effect” (Hauber, Sherman, & Paprika, 2000; Hauber & Sherman, 2001). Hauber et al. (2000) suggest that despite being reared with other species, inter-specific brood parasites, such as the brown-headed cowbirds in their study, can still identify members of their own species. They suggest that these birds learn about aspects of their own phenotype and can later identify other members of its species by similarity to itself. In the first experimental manipulation of a recognition cue in self-referent phenotype matching, Hauber et al. (2000) used coloured markers to colour the feathers of cowbird fledglings in an experiment using a repeated measures design. In a simultaneous choice situation between normal coloured and adult female stimulus objects that were coloured with coloured marker, the subjects approached and spent more time near the adults that were similarly coloured.

Hare, Sealy, Underwood, Ellison, and Stewart (2003) take issue with Hauber et al.’s (2000) findings, stating that their study does not provide definitive evidence of self-referent matching. For example, the cowbirds used in Hauber et al.’s (2000) study were only removed from their hosts’ nests nine days after hatching, during which they were exposed to heterospecific and even possibly conspecific young, and they tested the same subjects repeatedly. Hare et al. (2003) also suggest that self-referent matching would be similar in effect to the product of genetically-based sensory biases, a mechanism that has already been demonstrated in mice. Hare et al. (2003) also suggest the importance of the natural context in interpreting Hauber et al.’s (2000) findings. Hare

et al. (2003) point out that although juvenile male cowbirds express a range of feather colours early in life, and have supposedly formed a template based on their own colouration, they are still able to identify conspecifics later in life—conspecifics that would not match their self-referencing template.

The role of individual recognition does not seem to be as important in ducklings as it is in other species. For example, individual recognition may play more of a role in species with social hierarchies. Goslings can recognize siblings at an early age as rank order in family groups is established during their first week of life (Radesäter, 1976). Shapiro and Bruce (1977) have shown that mallard ducklings can distinguish between their own mothers and strange mothers, but prefer a brood of ducklings to their own mother in their first week of life. Whatever role individual recognition plays in the mallard duckling, the number of siblings or peers appears to be more important than particular siblings or peers (Bruce & Shapiro, 1977a; Darczewska & Shapiro, 1999).

IMPRINTING

Konrad Lorenz (1935/1957) is credited with coining the term imprinting in describing the process by which young birds form attachments. In this thesis, the term imprinting will be used as it was originally defined, but its use should not be taken as acceptance of the concept. Using the term “imprinting” reifies the concept and results in researchers committing a nominal fallacy; that is, the phenomenon is named but it is not explained. For example, referring to a stimulus that a subject is exposed to and is presumed to form an attachment to as an “imprinting stimulus” suggests the acceptance of a phenomenon even as researchers are conducting experiments to determine if the

phenomenon actually exists. This “imprinting stimulus” is more accurately defined as a training stimulus. Training stimulus is an objective term that does not make any associations with the term “imprinting”.

The term “imprinting” implies a process that takes place within an individual and is not observable. Most studies of attachment in the psychological literature have used the amount of time a subject spends with an object or the amount of time a subject spends following an object as a measure of that subject’s preference. Attachment is inferred from the subject’s observable behaviour, i.e., the subject’s preferences. The purpose of this study was to investigate a possible mechanism mediating these preferences.

Observations similar to what Lorenz referred to as “imprinting” have been known for many years. Pliny the elder (A.D. 27, as cited in Hess & Petrovich, 1977) observed that geese could form a persistent attachment to humans. Spalding (1873) published the first scientific experiments on what he called instinctive behaviour. Spalding placed hoods over chicks’ heads to limit their visual experience. He stated that chicks had an instinct to follow and that this instinct would be expressed in the presence of the first object it sees. He found that when a chick was un-hooded at four days of age, it expressed “fear” of the experimenter instead of coming to follow him as the chicks that were un-hooded at a younger age did. He also noticed that once a chick came to follow the experimenter, transferring this following instinct back to the subject’s original mother was very difficult.

Lorenz (1935/1957) based his imprinting hypothesis on naturalistic observations, as well as on planned and chance experiments on a large number of species that he possessed over many years. He stated that although the process of “imprinting” was

innately determined, the object of the instinctive social reaction was acquired. For example, Lorenz was particularly interested in the fact that "isolated hand-reared individuals of most bird species do not recognize conspecifics as their own kind when introduced to them later" (Lorenz, 1970, p. 124). The mechanism seemed to be innate, but the object had to be learned.

Lorenz (1935/1957) stated that "imprinting" was fundamentally different from a learning process. Two characteristics separated it from learning. One characteristic of "imprinting" is that it can only occur at a certain time after hatching, or during a "critical period," (p. 104) and may occur with only one exposure (p. 107). Another characteristic is that the process appears to be irreversible; once a hatchling is "imprinting" to an object, this attachment cannot be undone (p. 119). He stated that although "imprinting" is often effected through the parents and siblings, it also determines the hatchling's behaviour towards others in its species. Therefore, only supra-individual properties of its family members are "imprinted" permanently. These properties are "imprinted" at a very early age, but also determine sexual behaviour later in development (p. 109). The most important characteristic of the object being "imprinted" upon is that it moves; it need not be alive. Also, "imprinting" can take place on relatively inappropriate objects, but the "imprinting" subject can become "imprinted" on a more appropriate object at a later time (p. 107). The reverse situation is not true, i.e., a duckling can be "imprinted" on a live model after it has been "imprinted" on a moving box, but it cannot "imprint" on a moving box after it has been "imprinted" on a live model.

Basic technique

The following response has been used in the laboratory to explore a wide-range of stimuli in place of the mother and brood (Bateson, 1966; Sluckin, 1973). The traditional "imprinting" experiments generally included a training session and a testing session. Subjects reared in isolation or communally were trained individually to the "imprinting" object, usually at 12-30 hr of age, for a short period of time. During the subsequent testing session, usually 24 or 48 hr later, individual subjects were again exposed to the "imprinting" object, which was usually a moving model to see if they would follow it. Whether or not the subjects followed the model was taken as evidence that "imprinting" took place. Much of this research focused on the importance of the mother.

Early studies into the basic principles of imprinting

One of the first systematic studies of "imprinting" was conducted by Ramsey (1951). Ramsey studied several species of ducks and many strains of chicken to determine some of the variables important in "imprinting". He found that colour seems to be important in recognition, while size and form is of less importance. He also noticed the important role of audition.

Ramsey and Hess (1954) outlined an experimental technique for studying "imprinting". What would later become known as the "Hess imprinting apparatus" consisted of a circular runway in which a model, suspended from an elevated arm radiating from the centre of the runway, could be moved around the runway remotely. The model was typically a mallard decoy fitted with a speaker and heating element.

A great deal of "imprinting" research began in 1956. One early researcher who studied the parameters of "imprinting" was Julian Jaynes (1956, 1957, 1958a, 1958b). These experiments were conducted using a 10 ft runway in which a looped cord passed around two pulley wheels located at either end. Models such as coloured spheres and cubes could be suspended from the cord and moved around the runway remotely, similar to the Hess apparatus. Jaynes (1956) measured the development of the following response in domestic chickens. He found that the following response, a response made without observable reinforcement, improves rapidly over the first four days of life. Jaynes' (1957) findings supported Lorenz's notion of a critical period. He found that younger chicks are more likely to be "imprinted" than older chicks. However, if "imprinting" does occur in older chicks, the following response is much more vigorous. He also found evidence of latent "imprinting" whereby a subject that does not react immediately after exposure does so at a later time. Contrary to notions that practice had no effect on the strength of which a chick may be "imprinted", Jaynes (1958a) found that practice, exposing subjects to the "imprinting" stimulus for a longer time, has a positive effect on following. Chicks, when exposed to both the "imprinted" object and a strange stimulus, show fewer generalized responses to the strange object over time and come to follow the "imprinted" object more and more. Jaynes (1958b) referred to this adjustment in the chicks' preferences in the absence of differential reinforcement as "emergent discrimination."

Moltz and Rosenblum (1958a, 1958b), and Moltz, Rosenblum, and Halikas (1959) conducted several experiments testing the hypothesis that the following response is a positive function of "anxiety" present during testing. In the first study, Moltz and

Rosenblum (1958a), using an apparatus similar to Jaynes (1956), found the following response decreased in the Peking duckling over a 15-day period. This result is contrary to Lorenz's contention that "imprinting" was irreversible in its effect. Moltz and Rosenblum (1958b) found that decreasing "fear" in the subjects by allowing them to habituate to the testing apparatus before testing lowered following during testing. In a third study, Moltz et al. (1959) found that increasing "anxiety" with shock increased the following response.

Though Lorenz coined the term, Hess (1959a, b, 1964) popularized "imprinting" and added four more characteristics to its definition. Hess (1959a, b) found that two factors determine the maximum point of the critical period. He found that maturing motor ability increases "imprinting", while the subsequent development of fear responses decreases "imprinting". "Imprinting" efficiency tends to increase until 13 to 16 hr of age and decreases thereafter. Hess (1959a, b) also added the "law of effort" which states that the strength of "imprinting" is directly proportional to the amount of energy put forth by the duckling in following an object. The "law of effort" has been criticized by Moltz, Rosenblum, and Stettner (1960).

Hess (1959a, b) found several more differences between "imprinting" and associative learning, including the effects of the primacy and recency of events. The primacy effect refers to the tendency to remember earlier events because they have been rehearsed and committed to memory. The recency effect refers to the tendency to remember the most recent events because they are still in working memory (Carlson, Buskist, Enzle, & Heth, 2002). Whereas recency is usually more relevant to associative learning, Hess (1959a, b) found that primacy of experience, rather than recency, is more effective in "imprinting".

Hess (1959a, b) also stated that imprinting was different from associative learning because visual discrimination is quicker when subjects are trained with spaced trials rather than massed trials and because aversive stimuli increases rather than decreases the following response (Hess, 1959a, b, 1964). Hess (1964) also found some evidence of effects of early experience on factors other than attachment in what are referred to as “food” and “environmental imprinting.”

Irreversibility

There are many contradictory studies concerning the irreversibility of imprinting. The findings of Moltz and Rosenblum (1958a), using Peking ducklings, were contrary to Lorenz’s (1935/1957) contention that “imprinting” is irreversible. Hess (1959a) argued that some studies that support the irreversibility of “imprinting” have in fact examined the behaviour of ducklings that have gone past the critical period for “imprinting”. Thus, Hess said, studies such as Moltz and Rosenblum’s (1958a) are actually examining associative learning. However, Salzen and Meyer (1968) found that chicks in a simultaneous choice test at three days of age prefer a coloured object with which it has been reared, but come to prefer a different object in a subsequent simultaneous choice test after the chick has been reared with that object for three or six days.

“Imprinting” is also thought to affect later behaviour, most notably adult sexual behaviour (Lorenz 1937/1957). Most advocates of the irreversibility of “imprinting” point to studies in which the effects of “imprinting” early in life are manifested in adult sexual preference (Kruijt, Bossema, & Lammers, 1982; Klint, 1978; Schein, 1963; Sherrod, 1974). However, many of these studies included early experience outside of the

sensitive period for "imprinting", so whether the effect is truly due to what is deemed "imprinting" is questionable.

Sensitive period

Investigating the age when a young hatchling can approach and follow a stimulus resulted in the concept of a sensitive period. Jaynes (1957) tested the responsiveness of domestic chicks to moving objects. Seven groups of subjects were reared communally and they were exposed to a moving object at various ages ranging from 1-6 hrs post-hatch to 54-60 hr post-hatch. The subjects were tested individually and their responses to the moving object during testing were recorded during the final five minutes of their 30-min trial. He found that the older a chick is at first exposure to the "imprinting" stimulus, the less likely "imprinting" would occur. The tendency to follow decreased as the subjects' first exposure to the "imprinting" object approached 54-60 hr post-hatch. James (1960) found that chicks up to 24 hr of age approach a light source at first exposure more than chicks at seven days of age. Even though the findings of Jaynes (1957) and James (1960) differ, Sluckin (1973) states that differences in findings are common considering the differences between laboratory procedures and the types of stimuli used.

Lorenz (1937/1957) stated that "imprinting" susceptibility is limited to a certain time after hatching. Many researchers examining this aspect of "imprinting" found the initial definition of this period too restrictive, referring to it instead as a sensitive period. Ramsey and Hess (1954) found that "imprinting" susceptibility in mallard ducklings ranged from a period from five to 24 hr post-hatch, with maximum susceptibility between 13 and 16 hr post-hatch. Gottlieb (1961a) defined the critical period in white Peking ducklings in terms of developmental age, defined as the age of the duckling from the

onset of incubation. Ducklings hatch out between the 26th and 27th developmental day of incubation (Gottlieb, 1961a). Gottlieb (1961a) did not find a critical period using the traditional measure of post-hatch age, but did find one using the more sensitive measure of developmental age. The 27th developmental day corresponds roughly to the first day post-hatch. He found that for hatched ducklings, the critical period for visual “imprinting” occurs on the 27th day after the onset of incubation. Ducklings exposed to a training stimulus on the 27th day from the onset of incubation exhibit the highest rates of following when tested at a later time. Ducklings that were trained on the 26th and 28th days after the onset of incubation followed the training stimulus much less than the ducklings trained on the 27th day from the onset of incubation. Gottlieb and Klopfer (1962) found that ducklings trained to a stimulus before the 27.5th day after the onset of incubation (i.e. day 26.5 to 27.5) exhibited a greater sensitivity for what they termed auditory “imprinting”. Ducklings trained after day 27.5 after the onset of incubation (i.e. day 27.5 to 28.5) showed a greater sensitivity for what they called visual imprinting.

End of the sensitive period

In reviewing the studies that examine the termination of the sensitive period, Kaufman and Hinde (1961) classify them into four categories. The first category included studies that state that “imprinting” sensitivity is brought to an end by maturational factors (Guiton, 1959; Jaynes, 1956; James 1960). The second category involves the development of fear responses. The result of the onset of fear is such that the hatchling no longer approaches a stimulus and instead moves away from it, negating the possibility of “imprinting” (Guiton, 1959, Hess, 1959a; Sluckin & Salzen, 1961). The third category states that socialization inhibits susceptibility to “imprinting” (Guiton, 1959; Hess,

1959a, b). The inhibition may be an effect of imprinting onto conspecifics (James, 1960). The fourth category includes studies that find that the sensitive period is the end of a state of low anxiety of the individual, which is a necessary condition for imprinting to take place (Moltz & Rosenblum, 1958b). Kaufman and Hinde (1961) suggest that these explanations for ending the sensitive period may be due to the different experimental situations and due to the various species being used.

CRITICISM OF IMPRINTING

Early on in the “imprinting” literature researchers were aware of the problems and limitations of their methods. Jaynes (1957) stated that his findings are only applicable to the conditions of each experiment. Species differences, the nature of the imprinting stimulus used, and the duration of the “imprinting” session were thought to be factors in interpreting the results of “imprinting” experiments (Sluckin, 1973). Thus, generalizing between experiments and the species used is very difficult (Sluckin, 1973).

Moltz and Rosenblum (1958a) found that when neither primary or secondary reward is associated with the “imprinting” stimulus, “imprinting” appears to be an unstable phenomenon. Gray (1961) studied the effects of colour in “imprinting” experiments and took issue with the fact that there were no standardized colours to control for an unlearned colour bias. Gray (1961) suggests that an unlearned bias may be why some experiments get a poor response from their subjects (i.e. Moltz & Rosenblum, 1958). Colour biases have been shown in other avian species such the canary (Kilner, 1997) and the barn swallow (Saino, Ninni, Calza, Martinelli, De Bernardi, & Møller, 2000). Barn swallows preferentially feed chicks whose gaping mouths are a brighter red

than others. The red colour is due to the presence of carotenoids, which contribute to pigment molecules and also aid in immune function. A brighter gape suggests healthier offspring since they can allocate carotenoids to pigmentation rather than to immune function. Investing more in healthy offspring provides the parents with greater long term payoff (Saino et al., 2000).

Inappropriate subjects

The subjects used in “imprinting” experiments may also have been a factor leading to inconsistent results. For example, domesticated forms of a wild species may yield inconsistent behaviour. Moltz and Rosenblum (1958) found that White Rock chicks exhibit a preference for red rather than white; a finding that is counterintuitive, considering that the White Rock chicken is itself white. Gray (1961) stated this finding is not surprising, since the ancestral form of this chicken (*Gallus bankiva*) has a red breast. Thus, the chickens were exhibiting a preference for its ancestral form. Shapiro (1977) obtained similar results from White Peking ducklings, which show a preference for the rouen duck to a female of its own breed. Because of the occurrence of ancestral preferences such as these, it has been suggested that the wild form of the organism be used in avian attachment research (Shapiro, 1977, 1980a; Wereha & Shapiro, 2003).

Inappropriate stimuli

Shapiro (1977) observed that ducklings follow their mother in the natural environment but that this behaviour is not consistently observed in the laboratory. Shapiro (1977) suggests that some aspects of the laboratory may be responsible for this inconsistency. He states that perhaps some of the necessary cues required for eliciting following have been eliminated due to the artificiality of the laboratory. For example,

many researchers used inappropriate, inanimate stimuli such as mallard decoys instead of live ducks. The argument for using biologically appropriate stimuli in the laboratory is best summed up by Shapiro (1970b):

The complexity of stimuli attending the formation of an attachment between parent and young seems enormous at best and too complicated to be understood at worst. To simplify this situation inside the highly controlled and often sterile environment of the researcher's laboratory seems inappropriate (p.2).

Shapiro (1977) argues that if "imprinting" is a form of dyadic stimulation, in which a stimulus comes to elicit a reaction from a subject, a live reactive model is required. In reference to the disparity between the conditions in the natural environment and the laboratory and the consequential and differential outcomes, Lickliter and Gottlieb (1986b) state "it is dismaying to think that after 50 years of research, we might be back to square one in our understanding of filial imprinting as it relates to events in nature" (p. 565).

Inappropriate terminology

Inappropriate terminology refers to the argument made on page 27, that by naming a phenomenon, it is "made real" and may lead researchers to believe that they have explained the phenomenon when they have only labelled it. Using the term "imprinting" leads researchers to accept the framework of "imprinting" without empirically testing the concept. By accepting "imprinting" as "real" researchers are committed to a certain perspective and may be oblivious to other interpretations of attachment behaviour or other factors which may be relevant mechanisms mediating an attachment.

Inappropriate rearing methods

Shapiro (1970b) also stated that inconclusive results in "imprinting" research could be due to the method of rearing subjects in isolation. "Imprinting" researchers reared subjects in visual isolation out of convenience and as a way to control the possibly confounding factor of experience. This strict laboratory control, which is greatly desired in most research, may have produced artificial results (Shapiro, 1970b).

Isolation and communal rearing is a most relevant factor when one is concerned with the social interaction between members in a brood. If "imprinting" is referred to as a form of dyadic stimulation (Shapiro, 1977), what are the effects of isolated rearing? Many researchers have found behavioural differences in subjects that were communally reared and those reared in isolation (Gottlieb, 1961b; Gottlieb & Klopfer, 1962; Guiton, 1959; James, 1960; Kruijt et al., 1982; Shapiro, 1980c). In terms of maternal "imprinting", the effects are so profound that Lickliter and Gottlieb (1986a) state "the relative permanence or irreversibility of maternal preferences reported in the vast imprinting literature might only be an artefact produced by the interpolation of social isolation between training (imprinting) and later testing in conventional laboratory studies of imprinting" (p. 266). There are profound implications associated with rearing subjects in social isolation in avian attachment research.

EFFECTS OF SOCIAL EXPERIENCE VS. ISOLATION ON PEER RELATIONS

The importance of early experience on behaviour has been well known for a long time (for example, see Beach & Jaynes, 1954, for review). Early social deprivation has been found to have a negative effect on many species, including chickens (Vidal, 1975),

red jungle fowl (Kruijt, 1964), rats (Day, Seay, Hale, & Hendricks, 1982; Gruendel & Arnold, 1969), and primates (Harlow & Harlow, 1962; Lewis, Gluck, Petitto, Hensley, & Ozer, 2000; Martin, 2002). Subjects in “imprinting” experiments were almost always reared in isolation and in the dark (Gaioni, DePaulo, & Hoffman, 1980). This method was suggested by Lorenz (1935/1957) because he believed that the behaviour of birds was purely instinctual and he downplayed the importance of learning.

However, several researchers have found that social rearing in “imprinting” experiments results in less responsiveness to the “imprinting” object (Guiton, 1959; James, 1960; Sluckin & Salzen, 1961). Guiton (1959) found that physical contact between a chick and an “imprinting” stimulus stimulates following. Further, he noted that isolated chicks follow an unfamiliar moving object for longer than socialized ones and that a single chick is more quickly attracted to a group of chicks rather than to a single chick. Guiton (1959) also stated that the onset of fear, which, reputedly, marks the end of “imprinting” susceptibility, is only applicable in completely isolated birds. Socialization seems to inhibit the following response to unfamiliar objects earlier than the onset of fear. Gottlieb and Klopfer (1962) found that socially reared Peking ducklings follow a training stimulus less than ducklings reared in isolation, while Hess (1964) and Polt and Hess (1964) found the opposite effect.

Differences in aggressive behaviour are also apparent in subjects reared in isolation or communally. Hoffman and Boskoff (1972) tested Khaki Campbell ducklings (*Anas platyrhynchos domesticus*) that were either reared individually and exposed every day to a training stimulus or reared socially in pairs and were not exposed to a training stimulus. On day 5 and 6 posthatch, a duckling that was reared in isolation and exposed

to the training stimulus and a duckling that was reared socially and that was not exposed to the training stimulus were placed together in a testing apparatus in the presence of the training stimulus. On day 6 of testing, measures of aggression were recorded. Aggression was defined as pecking of sufficient force to initiate flight on the part of the recipient.

Hoffman and Boskoff (1972) found that the ducklings that were reared in isolation and previously exposed to the training stimulus daily followed the training stimulus during the testing trial. The socially-reared ducklings that were not exposed to the training stimulus, however, paid little attention to the training stimulus and instead tried to stay near the duckling that was reared in isolation and previously exposed to the training stimulus daily. However, when the socially-reared ducklings attempted to approach the ducklings that were reared in isolation, the socially-reared ducklings were vigorously pecked by the ducklings that were reared in isolation and exposed to the training stimulus. The ducklings that were reared socially never retaliated and instead fled to the opposite side of the apparatus. The condition of isolated rearing seemed to elicit aggression in the ducklings. Aggression is rarely witnessed among ducklings that were socially reared.

When the training stimulus was withdrawn, the ducklings reared in isolation and exposed to the training stimulus daily showed a statistically significant increase in distress vocalizations and a statistically significant decrease in aggressive behaviour. When the socially-reared ducklings approached the ducklings reared in isolation when the training stimulus was absent, the ducklings reared in isolation would not show any aggressive behaviour and would, in fact, flee from the socially-reared ducklings rather than attack them. Hoffman and Boskoff (1972) suggest that the aggressive behaviour

exhibited on the part of the ducklings reared in isolation could be, in part, due to a fear reaction to the unfamiliar socially-reared ducklings.

Another study by Hoffman, Boskoff, Eiserer, and Klein (1975) verified the results of the previous study and found that ducklings reared in isolation or ducklings that were recently deprived of social contact exhibited high rates of aggression towards a conspecific. An interesting finding was that when the isolated duckling was not being aggressive during the trials, high rates of filial behaviour were observed. This result led the experimenters to refer to isolation-induced aggression as a reversible phenomenon. Also, this study does not support the notion that aggression is due to a lack of opportunity to dissipate an innate aggressive drive (Lorenz 1935/1957) but is due to a lack of stimulation from an object that would elicit filial behaviour (Hoffman et al., 1975).

Other behavioural differences may be apparent under these different rearing conditions. Sigman et al. (1978) found that Leghorn chicks reared in isolation or socially prefer socially-reared chicks in a preference test at 48 hr of age, suggesting something "appealing" in the behaviour of socially reared chicks. The role of social facilitation in feeding in chicks is well known (Tolman & Wilson, 1965) and may also have an effect on ducklings. Ducklings in isolation may eat less and may act differently. Klopfer (1959) stated that it is through social facilitation that ducklings in a brood come to act together as a unit.

So how do we interpret differences between studies that have utilized different rearing conditions? Shapiro (1972b; 1980c) found a difference in behaviour in Peking ducklings reared under isolated and communal conditions. From his interpretation of the observed behavioural differences, Shapiro (1972b) made two suggestions: 1) researchers

should manipulate rearing conditions in the natural environment to see what effect these manipulations have on the subjects, and 2) confine laboratory findings to the conditions under which the experiments were performed. Thus, “imprinting” experiments done in the laboratory may have limited generalizability to the natural environment. Studies conducted in the Avian Behaviour Laboratory at the University of Manitoba have attempted to approximate rearing situations that are more likely in the natural environment and, like others, have cast doubt on the validity of much of the “imprinting” literature (Bateson, 1966; Sluckin, 1973).

“PEER-IMPRINTING”

Some researchers have suggested that hatchlings may “imprint” onto each other (Collias & Collias, 1956; Guiton, 1959). Examining “imprinting” between peers necessitated their being reared together. The results of these studies contradicted much of the relevant literature and suggested the importance of rearing conditions on behaviour in avian attachment research (see Lickliter, Dyer, & McBride, 1993, for review). A series of experiments demonstrated the profound effect that social experience has on duckling behaviour (Johnston & Gottlieb, 1985a, b; Lickliter & Gottlieb, 1985, 1986a, b, 1987, 1988; Dyer, Lickliter, & Gottlieb, 1989) and raised interest in the notion of “peer imprinting” (Dyer, Lickliter, & Gottlieb, 1989).

These experiments were very similar in their methodologies. In all of these experiments, incubator-reared Peking ducklings (*Anas platyrhynchos*) were used as the subjects. After hatching, the subjects were placed in visual, but not auditory isolation, in a brooder until their “imprinting” trial. At 24 hr post-hatch, the ducklings were each given

a single 30-min "imprinting" trial, in which the ducklings were allowed to follow a stuffed model of a mallard hen emitting the mallard maternal assembly call. After the "imprinting" trial the ducklings were placed back into relative isolation (visual but not auditory isolation), or placed into a communal rearing condition with several other same-aged ducklings. The subjects were then tested in a 10-min trial at 48 hr post-hatch, and again at 72 hr post-hatch, for their preferences for various stimuli. The following is a synopsis of the most important studies demonstrating the importance of the brood to a duckling, as well as demonstrating how a brood affects an attachment to the hen.

1) Johnston and Gottlieb (1985a) tested subjects "imprinted" to the mallard model at both 48 hr and 72 hr of age for their preference for the familiar stuffed mallard hen model and an unfamiliar stuffed pintail (*Anas acuta*) hen model. Two trials were conducted. In one trial the models were silent. In the other trial both models emitted the mallard maternal assembly call. Based on a visual preference (silent models) the ducklings showed a significant preference for the familiar mallard model at both the 48-hr and 72-hr tests. When both models emitted the mallard maternal assembly call, no preference was found at the 48-hr test, but a preference for the familiar mallard model was found at the 72-hr test.

To test whether the change in preference between 48 hr and 72 hr was due to maturational changes or the experience from the 48-hr test, Johnston and Gottlieb (1985a) eliminated the testing trial at 48 hr and only tested the ducklings with vocalizing models at 72 hr of age. This change resulted in no preference for either model in the 72-hr test, suggesting that being exposed to the vocalizing models at 48 hr of age may have played a role in the duckling's ability to choose on the basis of visual cues in the second

test. To test this possibility, the 48-hr test was eliminated and the subjects were reared in a communal rather than an isolated situation between the "imprinting" trial at 24 hr and the testing trial at 72 hr. They found that the subjects preferred the familiar mallard model at 72 hr, suggesting that the 10-min experience of the 48-hr test was as effective as the 48 hr of social rearing in eliciting a choice in the 72-hr test. Their results suggest that visual, motor, and/or social experience between 24 and 72 hr is necessary for the ability to choose between the two models when the choice is based strictly on visual cues.

2) Johnston and Gottlieb (1985b) found that ducklings reared in isolation and exposed to the training stimulus at 24 hr of age do not show a preference for the silent familiar mallard model over a silent unfamiliar redhead model (*Aythya Americana*) at 48 and 72 hr. Communally-reared ducklings, on the other hand, were found to prefer the familiar mallard model at 48 hr of age. However, communally reared ducklings did not show a preference at 72 hr of age. This experiment demonstrated a difference between isolated and communally-reared subjects when it comes to maternal preferences for stuffed models. Johnston and Gottlieb (1985b) postulated that the effect of communal rearing may be transitory, hence the lack of a preference at 72 hr. Another experiment further tested whether or not later social experience interferes with visually "imprinted" preferences. It was conducted by providing social experience to the subjects only between the "imprinting" trial at 24 hr and the first trial at 48 hr and keeping the subjects in isolation between 48 and 72 hr. Eliminating this hypothesized source of interference should lead the subjects to prefer the familiar model at 72 hr. Indeed, subjects preferred the familiar mallard model to the unfamiliar redhead model at both 48 hr and 72 hr. These findings suggest that, contrary to the conventional "imprinting" literature,

continual exposure to the mother in the natural environment may be required to maintain the maternal bond due to interference from other brood members.

3) Lickliter and Gottlieb (1985) wanted to determine whether the ability for visual discrimination of the familiar mallard hen over the unfamiliar redhead model is due to the extra visual experience afforded by the social situation, or whether it is due to reciprocal social interaction. No visual preference was found for either the familiar mallard model or the unfamiliar redhead model at either 48 or 72 hr if; 1) the ducklings were denied physical contact with one other duckling but they could hear and see each other 2) the subjects were reared with only one other duckling, or, 3) the subjects were denied actual social interaction in a group of ducklings but they could hear and see them. A visual preference for the familiar mallard model at both 48 and 72 hr was exhibited if the subjects were permitted unrestricted social interaction with siblings. Thus, social experience provided by direct contact from siblings, as a duckling would experience in the natural environment, may help to strengthen the visual preference for a stuffed model. They state that the methods of studying "imprinting" in the laboratory (namely, rearing subjects in isolation) may not be appropriate for investigating the process of filial "imprinting" in the natural environment.

4) Lickliter and Gottlieb (1986a) investigated how social interaction with siblings during the "imprinting" trial affects attachment to the maternal stimulus. The "imprinting" literature states that if a duckling reared in isolation is exposed to an adult model of its own species shortly after hatching, it will exhibit a preference for the adult at a later time. Lickliter and Gottlieb exposed ducklings reared in isolation to a stuffed hen model at 24 hr post-hatch either alone or with four other ducklings. The ducklings trained

alone preferred the familiar maternal model over an unfamiliar pintail model and four stuffed ducklings at both 48 and 72 hr post-hatch. Ducklings trained with other ducklings preferred the stuffed duckling models over the two adult models at both 48 and 72-hr choice tests. Another experiment in this study tested untrained ducklings reared in isolation for their preference for the mallard hen model and the duckling models at 48 hr. No preference for either stimulus was exhibited, suggesting that the preference for the mallard model in the subjects reared in isolation in the first experiment was due to the training ("imprinting" session). These findings are in line with "imprinting" research conducted previously.

Johnston and Gottlieb (1985b) showed that communal rearing facilitated a preference for the familiar mallard model at 48 hr of post-hatch age, but may have provided interference for a preference for the familiar mallard model at 72 hr of post-hatch age. They postulate that the preference for the familiar mallard model was replaced with a preference for siblings. To test whether or not this was the case, ducklings were tested at 48 and 72 hr for their preference for the familiar mallard hen or ducklings. They found that communally reared ducklings "imprinted" to the familiar mallard hen preferred the ducklings at testing at both 48 and 72 hr. Lickliter and Gottlieb (1985b) state that these results provide striking evidence for the reversibility of the visually "imprinted" maternal preference in communally reared ducklings. Alternatively, these results may demonstrate an existing, natural, preference for a brood of ducklings.

5) Lickliter and Gottlieb (1986b) examined the effect of broodmates during an imprinting trial on establishing a visual maternal preference. Ducklings reared in isolation and trained individually to the mallard hen model at 24 hr post-hatch showed a preference

for the familiar mallard model over an unfamiliar pintail model or four stuffed ducklings at 48 and 72 hr of post-hatch age. Ducklings reared in isolation but trained with broodmates, however, preferred the ducklings to the familiar mallard hen model at both 48 and 72 hr. This study shows that even brief exposure to broodmates (in this case, 30-min during training) interferes with the establishment of maternal "imprinting" and produces a very strong preference for other ducklings.

6) Lickliter and Gottlieb (1987) looked at when social experience needs to occur in order to contribute to maternal "imprinting". They found that ducklings reared and trained in isolation can discriminate between the familiar mallard model and a redhead model at 48 hr only if they receive social experience with siblings after, or both before and after, the initial exposure to the mallard model. In contrast, ducklings reared with siblings before and not after the "imprinting" trial did not show a preference for the familiar mallard model. Also, ducklings did not show a preference for the familiar mallard model if they were tested one hour after training, regardless of their rearing condition. They refer to this phenomenon as "retroactive excitation", as the visual features required for visually discriminating between the mallard and redhead models only becomes consolidated after one hour.

7) Lickliter and Gottlieb (1988) examined the species-specificity of social experience required to enhance the response to the "imprinted" maternal model. The ducklings only showed a preference for the familiar mallard model at 48 and 72 hr if they were raised with other Peking ducklings and did not show a preference when they were reared with domestic chicks (*Gallus domesticus*) or muscovy ducklings (*Cairina*

moschata). This finding suggests the importance of species-specific social interaction. Social experience with other precocial species was ineffective.

8) Dyer, Lickliter, and Gottlieb (1989) found that siblings are a stronger stimulus during the early development of ducklings and that visual "imprinting" to the mother may only occur after nest departure. To test whether active following of the hen was required for maternal "imprinting", the ducklings were not allowed to follow the mallard model. Instead they were "passively" exposed to a vocalizing mallard hen model with siblings present (to recreate a normal brood situation) and reared together for 24, 48, or 72 hr after hatching. The fact that the ducklings did not choose either the silent familiar mallard model or the unfamiliar redhead model at either 24, 48, or 72 hr suggests that active following is necessary to develop a visual maternal preference.

Since the ducklings were reared with both siblings and the mallard model, perhaps the ducklings became passively "imprinted" (i.e. "imprinted" without a training session in which following was involved) onto one another and not the mallard hen model. Support for peer "imprinting" is provided by the finding that ducklings reared with siblings or reared with siblings and a vocalizing mallard model for 48 hr up to testing prefer stuffed ducklings to a stuffed mallard hen at this time.

It is possible that the preference of the ducklings during testing may be due to the non-interactive nature of the stuffed mallard model as opposed to the live interactive siblings in the rearing condition. However, ducklings reared with seven stuffed ducklings still exhibited a preference for stuffed ducklings to the familiar mallard model during testing. This result suggests that a minimum amount of exposure to other ducklings is required for passive induction of peer "imprinting" (Lickliter, et al., 1989).

Rearing subjects in a manner that is more akin to that which is found in the natural environment, i.e. communally, has been found to have similar effects on the maternal preference in bobwhite quail chicks (*Colinus virginianus*) (Lickliter, 1989; McBride & Lickliter, 1993). Blaich and Miller (1986) found that ducklings in a brood without a hen exhibit lower alarm call responsivity than ducklings reared individually and in isolation. Gottlieb (1991) found that social rearing could induce malleability in the duckling. In his study, socially reared ducklings exposed to the maternal call of the chicken prior to and after hatching came to prefer the maternal call of the chicken over that of the duck. Ducklings reared in isolation did not come to prefer the chicken call. This malleability appears to be elucidated by tactile stimulation, which Gottlieb (1993) suggests may provide an optimum low level of arousal. Hicinbothom and Miller (1999) state that tactile contact is not necessary for the induction of malleability in ducklings with respect to plasticity of vocal output.

“Peer-imprinting” researchers (Johnston & Gottlieb, 1985b; Lickliter & Gottlieb, 1985, 1986a, b, 1987) have made some strong comments regarding maternal “imprinting” such as suggesting “that the relative permanence of maternal attachments formed as a result of imprinting may be to some extent an artifact produced by the isolated rearing conditions used in most studies of imprinting” (Johnston and Gottlieb, 1985b, p. 270), and that “even mere visual exposure to siblings does away with the imprinted maternal preference” (Lickliter & Gottlieb, 1986b, p. 265).

The results of these studies clearly and explicitly demonstrate the pervasive attraction of ducklings to conspecifics. These researchers, however, still interpret these findings in relation to a duckling's attachment to the mother. Focusing on the brood itself may be a more productive approach, allowing one to better understand the dynamics involved in maternal and "peer imprinting".

THE PROBLEM WITH "PEER IMPRINTING"

A problem arises in some studies that examine differences between subjects reared in isolation or communally. Gaioni et al. (1977) explain that the general method of testing differences consists of rearing experimental subjects in isolation and control subjects communally. All subjects would then be tested individually on a particular task. The difference between the two groups is then attributed to the effects of isolation. The problem with this method is that a control subject from the socially reared group, tested individually, may not be emotionally "neutral". Thus:

it is not clear whether observed behavioural differences between animals which have been isolated for a prolonged period and animals which have recently been separated from their social group should be attributed to the effects of isolation, the effects of separation, or to some combination of these two effects (Gaioni et al., 1977, p. 342).

A logical solution to this problem forms the basis of this study. If studies examining the differences between subjects reared in isolation or socially are confounded by testing socially-reared subjects individually, how does one obtain an accurate depiction of the

behaviour of socially-reared ducklings? The answer to this question is to observe responses of a brood of ducklings to a particular stimulus.

TESTING THE PREFERENCES OF A BROOD

Any systematic description or analysis of “imprinting” must take into account the natural social context in which it occurs (Lickliter & Gottlieb, 1986a; Shapiro, 1980b). The social context of the duckling includes the brood.

Though the brood has been mentioned in avian attachment research, it has not been extensively examined. Reynolds and Lickliter (2004) recently tested bobwhite quail communally but were interested in individual measures rather than group measures. The most relevant study to the examination of the behaviour of the brood was conducted by Klopfer (1959). Klopfer (1959) noted that ducklings in the wild function as a unit. In other words, the ducklings interact in a fashion that minimizes individual differences in behaviour. Klopfer (1959) suggests that variation in duckling responses is prevalent across “imprinting” studies because ducklings cannot moderate each other’s behaviour.

Klopfer’s (1959) study of the brood

Klopfer (1959) trained “leaders” which were ducklings of different species “imprinted” to a sound-signal from the experimenter. The leaders were reared separately from the “followers,” which were the untrained ducklings. The followers were reared together and were not exposed to the sounds to which the leaders were “imprinted”. Between 24 and 72 hr of age, the followers were tested in groups of three to 13 ducklings. One to three leaders were also placed into the group of followers. The age of the ducklings was randomized so that the leaders could be older, younger, or the

middle-age of the group. Size was controlled for by using different species. The leaders could be smaller bluewing teal (*Anas discors*), much larger redheads (*Aythya Americana*), or intermediate-size scaup (*Aythya affinis*). Klopfer found that a single leader can induce three to four followers to move towards the sound-signal to which it is “imprinted”. Inducing a larger group of followers to move towards the sound-signal simply required more leaders at the same ratio. Klopfer (1959) stated that this behaviour, which caused the brood to act as a single unit, is purely mechanical in nature and referred to it as a type of pacemaker effect.

Klopfer (1959) stressed the functional significance of what he called an example of social facilitation. He notes that under laboratory conditions, only a certain proportion of the ducklings could be “imprinted” under the conditions of the experiment. However, through social facilitation, the ducklings all behaved as if they were similarly “imprinted”. Klopfer (1959) goes on to suggest that this phenomenon could be “an instance of balanced polymorphism on a behavioural level” (p. 100).

Methodology for testing the preferences of a brood

Klopfer’s (1959) findings provided Wereha and Shapiro (2005) a basis to form a methodology for testing the preferences of a brood that could be easily employed in experiments conducted in the Avian Behaviour Laboratory. Wereha and Shapiro (2005) tested broods of 10 ducklings for their preference for another brood of 3 ducklings or no stimulus for eight 15-min trials each day for seven days (for a detailed description, see p. 70). In this experiment, mallard ducklings were examined on a square sand-covered table inside a sound-deadened experimental chamber (see details in apparatus and procedure section in the General Method, p. 64). The table was divided into four quadrants. A

stimulus brood of 3 ducklings was placed in a retaining pen in one of the four quadrants while the brood of 10 ducklings was permitted to move about a large portion of the table in a larger retaining pen that overlapped all of the quadrants. The time the 10 subjects spent in each quadrant was recorded. The stimulus brood's location was changed after every trial. Two different experimental broods of 10 subjects each ($n = 2$) were tested eight times each day for seven days.

Though the number is arbitrary, the experimenters agreed that the behaviour of the majority of ducklings (i.e. 7 out of 10 ducklings) would be representative of the behaviour of the brood as a whole, especially considering the synchronicity of duckling behaviour (Klopfer, 1959; Klopfer & Gottlieb, 1962; Sowls, 1955). Although 10 ducklings were being tested simultaneously, the location of the brood was defined as the quadrant occupied by at least seven of the 10 ducklings. The time spent in this quadrant was recorded. Based on Guiton's (1959) finding that chicks moved around his experimental runway slowly and as a group, this method of defining the brood seemed appropriate. It would provide an easily observable criterion for determining the location of the brood, especially considering the large number of ducklings being tested simultaneously. This method also provides a single score for time spent in each quadrant for each brood during each trial, facilitating data entry and analysis. Reynolds and Lickliter (2004) tested groups of four subjects for trials of two minutes each. The subjects were tested in a small plastic tub that had a grid pattern of string overlaid on the top of the tub effectively dividing the tub into six equal rectangular areas. A camera recorded each trial directly over the tub so behaviour could be scored at a later time. Their measures included grid crossing and huddle duration individually determined for each

subject being tested. Though this methodology is similar to what Wereha and Shapiro (2005) formulated, it records the behaviour of an individual rather than of several individuals simultaneously. The methodology of Reynolds and Lickliter (2004) would be too time-consuming and difficult given the number of subjects and length of trials used by Wereha and Shapiro (2005).

Results of the methodology

Wereha and Shapiro (2005; p. 70 of this thesis) found that the behaviour of seven out of 10 ducklings was representative of the behaviour of the brood as a whole (for more information see p. 72). In fact, the ducklings spent most of their time during testing together in the same quadrant. Though the criterion could have been more restrictive (eight or nine, or even 10 out of 10 ducklings), seven prevents the preference of the majority being skewed by the occasional straggler or “curious” duckling.

The importance of peers and siblings (i.e. other ducklings) has been shown to be important in laboratory and naturalistic studies. The methodology designed by Wereha and Shapiro (2005) represents an opportunity to examine a previously neglected area of avian attachment research.

THE PURPOSE OF THESE EXPERIMENTS

As previously indicated, the attachment between the mother and a hatchling has received much attention in the imprinting literature. The results of these studies are questionable for many reasons, the most relevant of which is that individual ducklings, reared in isolation and tested in an artificial environment using inappropriate stimulus objects, yields misleading results with respect to what actually occurs in the ducklings’

natural environment. Other studies (Bruce & Shapiro, 1977a; Johnston & Gottlieb, 1985a, Lickliter & Gottlieb, 1985, 1986a) have not focused on the mother and have found that peers and siblings are highly attractive to a single duckling. Single ducklings rarely occur in the natural environment and, it is assumed, never survive (Seymour, 1982). The next question that arises, then, concerns the preferences of more than one duckling, i.e. the brood. Most notably, does a brood of ducklings exhibit the same preferences that individual ducklings do?

A brood serves as a highly attractive stimulus to a duckling. A brood may satisfy the needs of a duckling whatever those needs may be (i.e. warmth, safety). Studies conducted in the natural environment have found that broods are very cohesive (Collias & Collias, 1956) and that lost ducklings attempt to join broods other than their own (Raitasuo, 1964). The largest brood has been shown to be preferred by a single duckling (Bruce & Shapiro, 1977a, Rogan & Shapiro, 1972, 1974). Wereha and Shapiro (2005) have developed a method of measuring the responses of a brood. The purpose of these experiments is to use that method to examine the brood size preferences of a brood for other broods of various sizes. These experiments were conducted to establish the importance of broods to ducklings, to compare and contrast the results of these experiments to the results of experiments testing single ducklings, and to contrast these results to that of the "imprinting" literature stressing the importance of the mother in the attachment process.

GENERAL METHODS

Subjects

Egg source. The subjects were 430 mallard ducklings (*Anas platyrhynchos platyrhynchos*). Eggs were obtained from an indoor flock in the Avian Behaviour Laboratory in the Department of Psychology at the University of Manitoba in the spring and fall of 2005.

The flock was hatched in the spring of 2003 and consists of 50 adult mallard ducks with a 1:4 ratio of males to females. The ducks come into two breeding seasons (one in the fall and one in the spring) with the use of a reverse lighting schedule. The flock's shortest day (8 hr) occurred on February 1, 2005. Day length was increased in 15-min intervals to the peak of 16.5 hr on May 10, 2005. A similar schedule was employed in the fall with August 10, 2005, and November 10, 2005, being the shortest and longest days, respectively. By laying time in the spring of 2005, the flock was about 1 year 10 months old and was laying for its third breeding season. In the fall of 2005 the flock was about 2 years 4 months old and laying for its fourth breeding season.

Fresh water to drink and to bathe in is constantly available to the ducks in a stainless steel tank containing 920 L of water. The surface area of the water is 3 m². The water is completely replenished every hour. Food is provided ad libitum for one hour in the morning and one hour in the afternoon. As the ducks began demonstrating breeding behaviours their food was gradually changed over from 15% Developer to 18% Breeder pellets from Feed Rite (17 Speers Road, Winnipeg MB, R2J 1M1). The floor of the aviary is covered with wood shavings and is changed once per week. Ten orange plastic

balls are placed throughout the aviary. The balls are used to discourage the ducks from pecking at any eggs that are laid outside of the nest boxes.

Incubation. Eggs were collected daily, washed, and placed in a cooler for up to one week. After this time the eggs were removed from the cooler and were allowed to warm up to room temperature. Cooling the eggs for at least 24 hr ensures that all the eggs being set in the incubator are at the same developmental age (Gottlieb, 1963). The eggs were set in a Petersime Model #1 incubator (Petersime Incubator Co., 300 North Bridge, Gettysburg, OH 45328) for 24.5 days at 37.5°C with 90-95% relative humidity. The eggs were cooled and sprayed with lukewarm water once a day to simulate natural incubation conditions. The inside of the incubator was also sprayed whenever its doors were opened to compensate for lost moisture. The eggs were candled once a week to monitor development of the embryos and to discard any infertile or cracked eggs and embryos that had died.

Hatching. On day 24 of incubation, the eggs were removed from the incubator and placed into a Petersime Model H145 hatcher where the ducklings were monitored until hatching was completed. Temperature in the hatcher was reduced from 37.5°C to 36.5°C once pipping had commenced. The relative humidity in the hatcher was kept between 86% and 90%. The hatcher was checked every two hours, 19 hr after pipping began, so that the age of each duckling was accurate within two hours. Hatching was defined as having occurred when the duckling had completely separated itself from the shell without any intervention by the experimenter. Hatchlings were removed, in the dark, once they were dry.

Leg banding. The ducklings were randomly divided into stimulus objects and experimental subjects and placed into brood units as soon as they were relatively dry after hatching. Randomization was accomplished through the use of a random numbers table. Usually the ducklings were dry in four to six hours after hatching and were transferred at this time. A coloured plastic leg band (red, pink, yellow, or blue in Experiment 1; green in the subsequent experiments) from the National Band and Tag Company (721 York St., Newport, KY, 41072) was placed on the right leg of each subject when it was transferred from the hatcher to a brood unit. Two experimenters were employed in tagging; one to hold the duckling and one to unfurl each band and place it around the duckling's leg. Tagging was conducted in the dark to minimize exposure of the experimenter to the ducklings. Graves and Siegel (1968) found that handling chicks had little effect on them if handling was done in the dark. A dot of acrylic paint (white, yellow, gold, pink, red, blue, or green) was placed on the top of each duckling's head (Wereha & Shapiro, 2005; Nietfled, Barrett, & Silvy, 1994) to facilitate the identification of individuals should they have lost their leg band. The ducklings were placed in an opaque 29.0 x 24.0 x 14.0 cm wooden transport box and taken to the brooding room. The bottom of this box was lined with wood shavings to provide traction and cushioning for the ducklings during transport.

Rearing conditions. Subjects were reared in a Petersime Model 2S-D brood unit. This brood unit contains 12 compartments, each measuring 100 x 70 x 24 cm. The floor is made of 1.5 cm mesh that allows waste to fall through and be collected in a tray below. Food and water troughs are located along two sides of the brood unit. Food and water were replenished as required. The ducklings were fed non-medicated 21% protein chick starter obtained from Feed Rite. Ducklings were able to thermoregulate by moving

towards or away from a centralized heat source. The temperature near the heating source was monitored and kept at approximately 32°C on the first day of the experiment and was gradually decreased to 30°C by the end of the seven day testing period. The temperature of the brooding room was maintained at 30°C. The lights in the brooding room were set on a 16:8 (hour) light/dark cycle. The lights were on in the room from 06:00 to 22:00 hr CST to approximate a normal day in the early summer and to allow for several testing sessions during the day.

Experimental subjects. A total 290 ducklings were used as subjects in these experiments. In the first experiment, 28 subjects were reared communally, in the light, in two broods of 14 subjects each (10 experimental subjects and four subjects raised as spares). In the second experiment, 96 subjects were reared communally, in the light, in eight broods of 12 subjects each, in eight separate compartments of the brood unit. In the third experiment 86 subjects were reared in two broods of 12, two broods of 11, and four broods of 10 ducklings each. In the fourth experiment, 80 subjects were reared in eight broods of 10 ducklings each. Each brood was reared in visual, but not auditory isolation from the other experimental broods and the stimulus objects. Although not the ideal situation, rearing subjects in visual but not auditory isolation is a practical and common procedure in avian attachment research.

In the first experiment, two groups of 10 experimental subjects were tested eight times each day for seven days. Each testing trial lasted 15 min. In the second, third, and fourth experiments, eight groups of 10 subjects each were tested for their brood size preferences once a day for seven days. Each testing trial lasted 15 min. Each duckling was identified by its leg tag and/or by its paint mark. The remaining subjects in each

brood unit served as spares. Dzubin and Gollop (1972) state that ten is a common brood size in the natural environment, where broods range in size from 5.7 to 10.6 on average (cited in Drilling et al., 2002). Testing the subjects for seven days is arbitrary but is used because it corresponds roughly to the first phase of plumage development in ducklings (Gollop & Marshall, 1954, as cited in Shapiro, 1977). Although most "imprinting" studies only test subjects at two or three days of age, Shapiro (1977) argued that development is continuous and should be looked at over a longer period of time.

Stimulus objects. A total of 140 ducklings were reared as stimulus objects in these experiments. In the first experiment, six ducklings were used to form a stimulus brood of three ducklings. The remaining three ducklings served as spares. The first experiment was conducted over two weeks, resulting in a total of twelve ducklings being reared as stimulus objects. The second experiment required 30 ducklings. This experiment, like the ones following it, was conducted over two weeks in order to obtain the number of ducklings required. Fifteen ducklings were reared each week. Twelve ducklings were required to form the two broods of three and nine used in the testing situation. The remaining three ducklings during each week were used as spares. The third experiment was a replication of the second experiment and required a total of 28 ducklings. Twelve ducklings were reared as stimulus objects in the first week, and 16 were reared in the second week. Twelve ducklings were required each week to form the stimulus broods of three and nine ducklings in the experiment. The four extra ducklings reared in the second week of the experiment were used as spares. The fourth experiment utilized a total of 70 ducklings. Thirty-four ducklings were utilized in the first week and 36 ducklings were utilized in the second week. During each week of testing, 29 ducklings were required to

form the stimulus broods of three, nine, and 17 ducklings. The extra ducklings reared each week were used as spares. The stimulus objects were reared communally, in the light. Each brood reared as stimulus objects was raised in visual but not auditory isolation from the experimental broods in other compartments of the same brood unit.

Randomization of subjects. Randomization was accomplished by using a table of random numbers with a few restrictions. One restriction was that ducklings were randomized with respect to assignment to groups in such a way that the average age of the ducklings in the brood occurred during the daylight hours (06:00 to 22:00 hr CST). Ducklings are diurnal organisms meaning that they are active during the day and sleep at night. Subjects were selected such that the mean age of the brood occurred during daylight hours. Ducklings hatched too late into the night or too early in the morning were used as spares or stimulus objects instead of subjects. Besides minimizing the probability of a time of day effect (Radford, Ng, & Armstrong, 1981; Bunsey, Sanberg, & Coyle, 1986), this restriction had the added benefit of convenience to the experimenter, since testing could be conducted during the day.

Another restriction was on the range of the ages of the ducklings used. Because hatching can take up to 48 hr, the range of the ages of the ducklings was minimized as much as possible to help ensure that the mean age of the group was a relatively accurate representation of the actual age of each duckling. The incubation procedures employed in the Avian Behaviour Laboratory have been perfected to the point that ducklings generally hatch during the day and within a 24 hr period, negating the need to employ these restrictions on duckling use.

Apparatus

The experimental chamber is a 2.4 x 2.4 x 2.0 m sound-deadened, heat-controlled room. Inside the chamber is a 1.5 x 1.5 m sand-covered table (Figure 2). A barrier made of wood and 1.0 cm wire mesh extends to a height of 21 cm above the surface of the table and prevents subjects from jumping off the table. The table is divided into four quadrants marked by shallow lines drawn in the sand. These quadrants are referred to as table quadrants. Retaining cages of 2.5 cm wire mesh measuring 40.0 cm in diameter and 45.0 cm in height located in each corner of the table were used to contain the stimulus broods. These cages are referred to as corner cages. Pieces of wire mesh measuring 29.0 x 10.0 cm are used to prevent the formation of corners where the retaining cages meet the wooden border. Ducklings have been shown to be attracted to corners (Darczewska & Shapiro, 1998).

Diffuse lighting in the chamber is provided by four 32 W fluorescent lights mounted on the walls near the ceiling. The ambient light intensity at the surface of the apparatus is approximately 700 lx. The temperature inside the chamber can be monitored from outside the chamber. The temperature in the chamber was maintained at 30°C.

A retaining pen of 2.5 cm wire mesh measuring 90.0 cm in diameter and 45.0 cm in height was located in the centre of the table where the table quadrants intersect. Part of each table quadrant was contained within this retaining pen (see Figure 2). This pen was used to confine the subjects comprising the experimental brood from the stimulus broods placed in corner cages in the table quadrants and was necessary to isolate the experimental brood from the stimulus objects. The experimental brood was placed in one

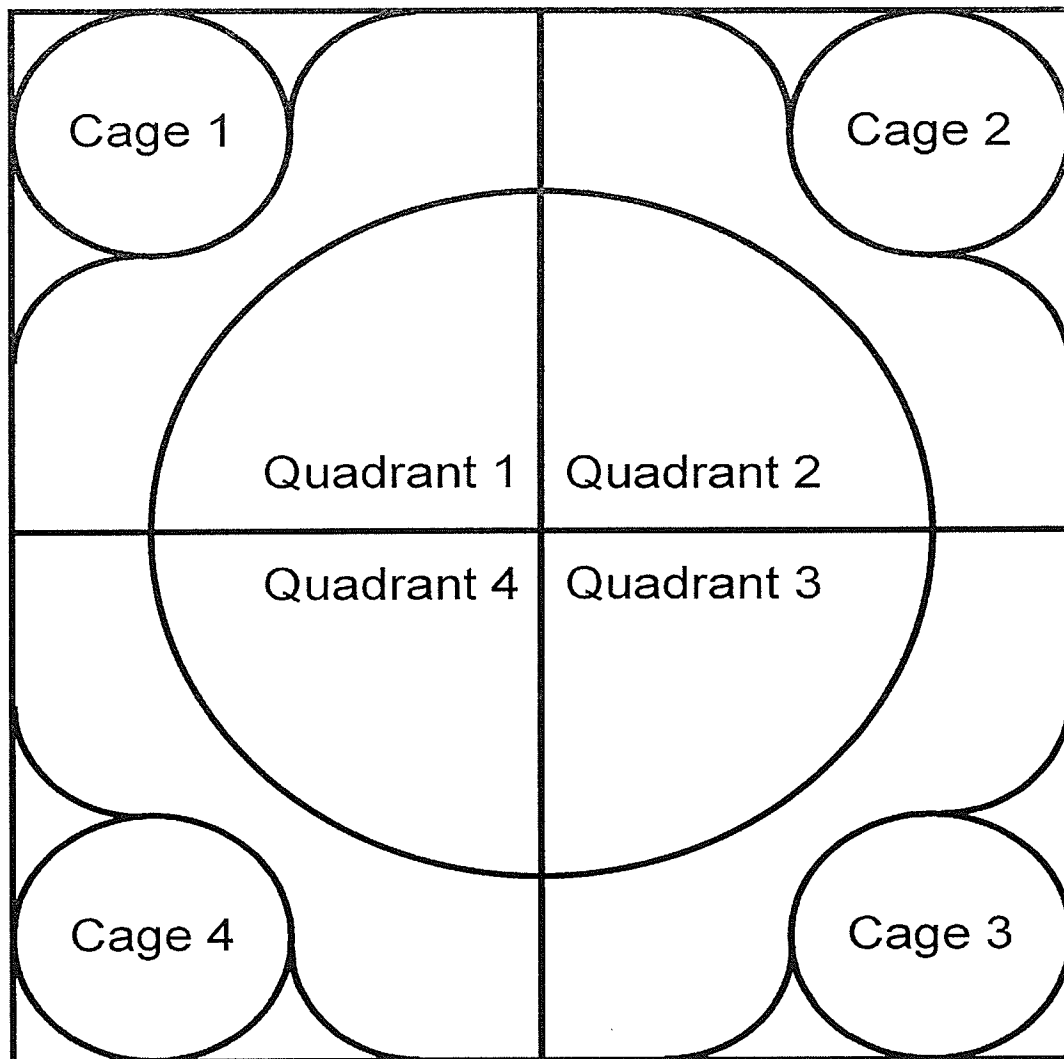


Figure 2. Overhead view of the experimental platform. The stimulus broods occupied the cages in the corner of the table. The experimental broods were placed in an empty quadrant within the large retaining pen in the centre of the table.

of the empty table quadrants within the large retaining pen, in the dark, at the beginning of every trial (see Figure 2).

The amount of time the experimental brood spent in each table quadrant was recorded. The table quadrant that the brood occupied was defined as the table quadrant that contained at least seven of the 10 members of the experimental brood (Wereha & Shapiro, 2005). Should the subjects have spread out over the sand-covered table such that fewer than seven subjects were in a single table quadrant, the experimenter would strike a key that stopped recording the time the brood spends in any table quadrant but allowed the 15-min time trial clock to continue to elapse. When at least seven of the 10 experimental subjects entered a table quadrant, time spent in that quadrant was again recorded. It was assumed that seven out of 10 subjects was representative of the brood as a whole and the location of the brood was recorded as the table quadrant in which the seven subjects were located (Wereha & Shapiro, 2005).

Latency, defined as the amount of time it takes seven out of 10 subjects to enter another table quadrant from their initial position, was also recorded. A Panasonic PVDV952 video camera was used in Experiment 1 to record each trial through a one-way vision window in case the data needed to be quantified differently.

Procedure

Testing (stimulus objects). Before testing began, the stimulus objects were removed from their communal brood unit, in the dark, and placed into a 29.0 x 24.0 x 14.0 cm wooden transport box. The stimulus objects were then taken to the experimental chamber where they were removed from the transport box, in the dark, and placed into a corner cage of a randomly determined empty table quadrant.

Testing (experimental brood). For testing, the experimental brood was removed from its communal brood unit and transported to the experimental chamber in the same manner as the stimulus objects. In the experimental chamber, the experimental brood was removed from the transport box, in the dark, and placed into a randomly determined empty quadrant within the large retaining pen in the centre of the testing table. Previous experiments in the Avian Behaviour Laboratory have tested individual ducklings by placing the subjects in the centre of the apparatus (without the large retaining pen in the centre of the testing platform). This procedure, however, could not be used with 10 ducklings. The experimental brood was always placed within the large retaining pen in a table quadrant not containing the stimulus objects. Placing the experimental brood in an empty quadrant within the large retaining pen provided a specific location from which the latency and choices of the experimental brood could be measured. It was assumed that if the experimental brood was attracted to the stimulus objects, it would leave its quadrant within the large retaining pen and move to a table quadrant containing the cage confining the stimulus objects.

In the first experiment, on the very first trial on each day, the experimental brood was placed in the large retaining pen in a quadrant opposite to the stimulus brood of three ducklings. Since only one experimental brood was tested each day for eight consecutive trials, the location of the stimulus brood of three ducklings was changed rather than the location of the experimental brood. The location of the stimulus brood of three ducklings was randomly rotated between table quadrants with the restriction that the stimulus brood would not occupy the same table quadrant that the experimental brood was currently occupying within the large retaining pen and that the stimulus brood would not occupy

the same table quadrant that it itself had occupied on the previous trial. The sand on the table was sifted after every trial.

In the second and third experiments, the first experimental brood was randomly placed in one of the two opposing empty quadrants within the large retaining pen. The placement of the experimental broods in subsequent trials was alternated such that an equal number of trials began in each empty quadrant. Each experimental brood had a stimulus brood to its right and to its left. The initial location of the stimulus broods and the empty quadrants was randomly determined with the use of a random numbers table each day.

In the fourth experiment, each experimental brood was placed in the one remaining empty quadrant within the large retaining pen. The location of the empty quadrant and of each stimulus brood was randomly determined each day.

The experimenter then exited the chamber and positioned himself in front of a one-way vision window next to a computer. A keystroke started the trial and turned on the lights in the chamber. The amount of time seven out of 10 subjects spent in each quadrant was recorded.

Time spent with models. The main dependent variable measured was an "approach and stay near" response. The amount of time seven out of 10 ducklings spent in each quadrant containing a stimulus brood was recorded. Other responses used as measures in other studies include approach and/or following, working for contact with a model, and distress upon withdrawal (Zajonc, Marky, & Wilson, 1974).

Number of entries. The number of times the brood entered each quadrant was automatically recorded by the computer and was used as a measure of general behavioural activity.

Latency. The brood's latency score is the amount of time it takes seven out of 10 ducklings to enter a quadrant from their initial position in the centre of the apparatus within the larger retaining pen. Low latency scores are usually an indication of a high level of responsiveness on the part of the subjects and of the biological appropriateness of the stimulus objects.

Behavioural notes. Detailed behavioural notes were made during each trial. These notes included information on general trends or special instances that may have had an impact on the other measures.

Statistical Analysis

In Experiment 1, a two-way analysis of variance with repeated measures on two factors (stimulus objects and days) was used to analyze the data. If a main effect was found ($\alpha = 0.05$), a post-hoc analysis was performed (i.e. pairwise comparisons). If an interaction effect was found, a simple effects analysis of variance was conducted. Since the other experiments were conducted over a two-week span, a three-way analysis of variance with a repeated measures design on two factors (stimulus objects and days) and a between subjects design on one factor (week-of-testing) was used on the data. If there was no main effect on the between subjects factor (week-of-testing), the data from both weeks of the experiment were combined and a two-way analysis of variance was run on the data in a similar fashion as described for Experiment 1. If there was a main effect for

the between subjects factor, the estimated marginal means from both weeks were examined to determine the cause of this effect.

In experiments done in the Avian Behaviour Laboratory in which single ducklings are tested, the measure of latency is used as a diagnostic tool and is not usually analyzed. The reaction time of the subjects to the stimulus objects is used as an indication of the health of the subjects and the appropriateness of the stimulus objects used. One of the hypotheses of Experiment 3 was that the broods in that particular experiment would have lower latency times than the broods in Experiment 2. In this case, the latencies were analyzed using a two-way analysis of variance with a repeated measures design on one factor (days) and a between subjects design on one factor (week-of-testing) to determine if there was a statistically significant difference in latency times between Experiment 2 and Experiment 3.

EXPERIMENT 1: IS AN EXPERIMENTAL BROOD OF 10 DUCKLINGS ATTRACTED TO A SMALLER STIMULUS BROOD OF THREE DUCKLINGS?

Much research has shown that a brood is highly attractive to a single duckling (Bruce & Shapiro, 1977a; Darczewska & Shapiro, 1997, 1999; Lickliter, Dyer, & McBride, 1993; Rogan & Shapiro, 1972, 1974; Shapiro, 1971). Broods are very cohesive and tend to act as a single unit (Klopfer, 1959; Klopfer & Gottlieb, 1962; Sows, 1955). Considering the mutual attraction that seems to exist among ducklings (Wereha & Shapiro, 2005), it was hypothesized that the brood of 10 ducklings would spend more time in quadrants containing the smaller stimulus brood of three ducklings than in quadrants not containing stimulus objects.

Methods

Subjects

Experimental subjects. Twenty-eight mallard ducklings were obtained in the manner described in the General Methods section. The ducklings were placed in one of two wooden brood units measuring 120.0 cm x 30.0 cm x 34.5 cm internally and were located in a temperature-controlled animal holding room. For a detailed description of the brood units see Shapiro (1970a) and Shapiro and Lundy (1974). These brood units had mesh floors to allow wastes to fall onto a tray below and were only used in Experiment 1. Two broods of 10 ducklings were tested eight times each day for seven days. The four remaining experimental subjects in each study served as spares. Only two broods were used in this experiment so that the experimenter could conserve subjects and test the proposed methodology. This experiment tested two different experimental broods of ducklings hatched one week apart.

Stimulus objects. The stimulus objects were 12 mallard ducklings obtained in the same manner as described in the General Methods section and reared communally in the same type of brood unit as the experimental subjects in this experiment. During each testing week, a total of six stimulus objects were reared. Three ducklings from the six ducklings raised as stimulus objects were randomly selected on each day of testing to serve as the stimulus brood. The remaining three ducklings served as spares.

Apparatus

The apparatus was the sand-covered table in the sound-deadened experimental chamber described in the General Methods section.

Procedure

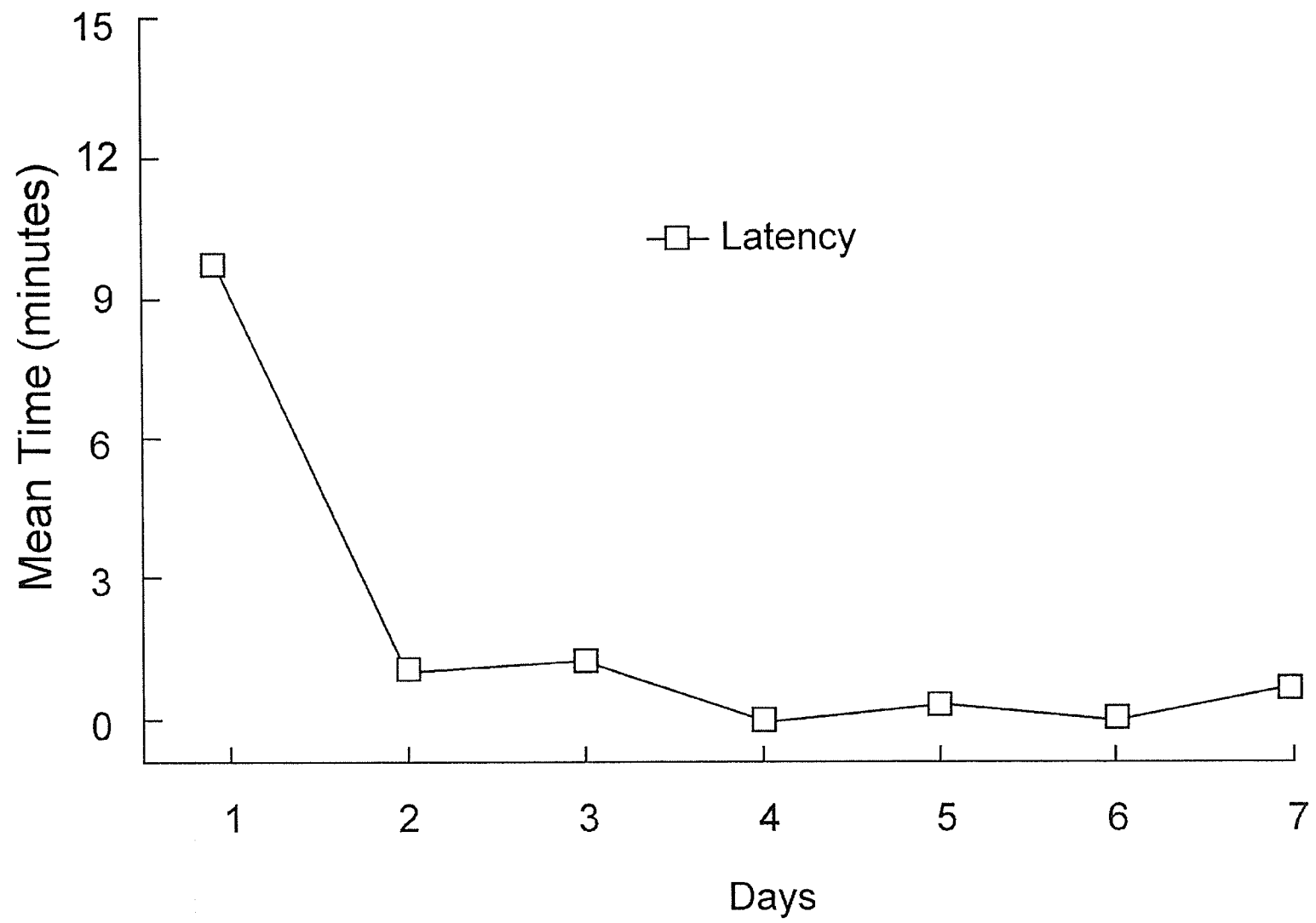
The stimulus brood of three ducklings was placed into a corner cage in a randomly determined table quadrant in the dark. The other three table quadrants remained empty. The experimental subjects were placed onto the sand-covered table in the large retaining pen in the dark. They were placed in the table quadrant in the large retaining pen that was opposite to the corner cage that contained the stimulus brood of three ducklings. The experimenter then left the room and positioned himself in front of the one-way vision window and the computer used to record the trial data. The 15-min testing trial began as soon as the lights were turned on in the chamber. After each 15-min testing trial was completed, the lights went out and the stimulus brood of three ducklings was placed into another corner cage in another table quadrant with several restrictions. First, the stimulus brood could not be placed in a corner cage in a table quadrant corresponding to the table quadrant in which the experimental brood was currently located in the larger retaining pen. Second, the stimulus brood could not occupy the same table quadrant that they had occupied in the previous trial.

Results

Latency is the amount of time the experimental brood took to move from its initial position into another table quadrant within the large retaining pen. Previous research has found that high latency scores indicate sick subjects or the presence of biologically inappropriate stimulus objects. Low latency scores indicate healthy, active subjects and biologically appropriate stimulus objects. In this experiment, as in previous studies, latency was used as a diagnostic tool. It was not statistically analyzed. Figure 3 shows the latency time of the experimental brood. The experimental brood appeared to be

Figure Caption

Figure 3. Mean time the experimental broods took to make a choice among quadrants in
Experiment 1



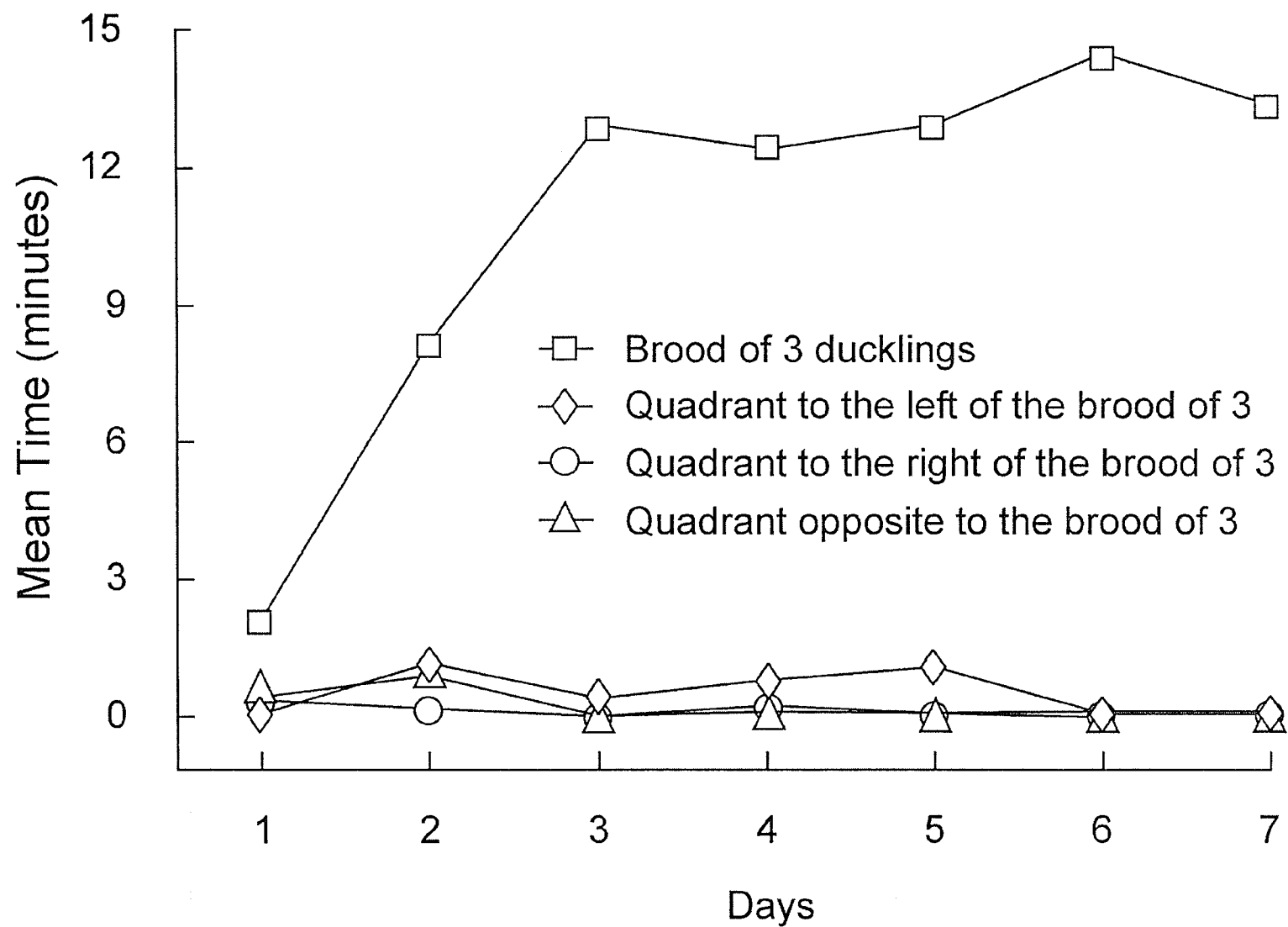
sleeping on Day 1 and, correspondingly, had very a high latency score on Day 1. On Days 2 to 7, however, the experimental brood became increasingly active and, hence, had a lower latency score. Figure 4 shows the mean amount of time the experimental subjects spent in each table quadrant. The ducklings spent an increasing amount of time near the stimulus brood of three ducklings over the first two days of the experiment. They then spent the majority of their time near the brood of three over the last five days of the experiment. By comparing Figures 3 and 4, it is evident that the dramatic drop in latency scores over the first two days of the experiment corresponds with an increasing preference for the brood of three ducklings. Over the majority of days the experimental broods very quickly approached the stimulus brood at the beginning of each trial. This situation resulted in a correspondingly low latency score.

A three-way analysis of variance with a repeated measures design on two factors (stimulus objects and days) and a between-subjects design on one factor (week-of-testing) was used to analyze the data. The mean time the experimental broods spent in each table quadrant in the large retaining pen on each of the seven days is illustrated in Figure 4. There was no main effect for week of testing ($F(1, 14) = 1.268, p = 0.221$, effect size or partial eta squared, $\eta^2 = 0.106$).

Effect size refers to the extent to which two variables are related. For example, a large effect size signifies that a large amount of the variability in one variable can be attributed to the other variable. Cohen (1988) stated that in the psychological sciences, the values of 0.10, 0.25, and 0.4 reflect effects sizes of small, medium and large magnitude, respectively. The measure of effect size, in combination with statistical significance, indicates the strength of a relationship between two variables. The

Figure Caption

Figure 4. Experiment 1: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing the stimulus brood of three ducklings or an empty quadrant.



between subjects factor of week-of-testing exists because two different broods were tested in two different weeks. Testing more than one experimental brood adds validity to the results of the experiment and increases the sample size but it also increases the variability of the data. The low effect size in this experiment, however, indicates that there is a weak relationship between Week 1 and Week 2. The statistical data revealed that the behaviour of the subjects was not significantly different between Week 1 and Week 2 in Experiment 1. On this basis, the data from both weeks of testing were combined and the combined preferences of the subjects for a brood of three ducklings versus an empty quadrant to the left, right, and opposite to the brood of three ducklings were analyzed over the seven-day testing period.

A test for sphericity was conducted prior to analysing the combined results. Sphericity refers to the assumption of homogeneity of within-group variances and is evaluated using Mauchly's test of sphericity. This test revealed a significant violation of the assumption of sphericity for days (Mauchly's $W(20, 170) = 0.037, p = 0.009$) and for stimulus broods (Mauchly's $W(5, 170) = 0.319, p = 0.013$). Violating the assumption of sphericity results in an increase in Type I error (rejecting the null hypothesis when it is, in fact, true, i.e. a false positive). To correct for this violation, the Greenhouse-Geisser correction was used. The original degrees of freedom are multiplied by the Greenhouse-Geisser correction. It adjusts for Type I error by lowering the degrees of freedom associated with the critical value, making the test more conservative. After this correction was applied, a two-way analysis of variance on days and stimulus objects revealed a significant main effect for stimulus objects ($F(1.747, 24.451) = 516.731, p < 0.001$, partial $\eta^2 = 0.974$) and days ($F(3.539, 49.550) = 17.024, p < 0.001$, partial $\eta^2 =$

0.549). A significant interaction was found between days and stimulus objects ($F(4.871, 68.193) = 11.459, p < 0.001$, partial $\eta^2 = 0.450$).

To investigate this interaction, a simple effects analysis of variance using six pairwise comparisons between the quadrant containing the stimulus brood of three and the three empty quadrants was performed on the data. Using six pairwise comparisons allows one to know whether one quadrant, be it an empty quadrant or the quadrant containing the stimulus brood, was preferred over the others. Because six pairwise comparisons were used, the critical value for each pairwise comparison was calculated by dividing the overall alpha level, $\alpha = 0.05$, by six, resulting in a critical alpha level for each comparison equal to or less than 0.0083. The interaction seemed to be due to a difference in preferences over the first two days of the experiment. On Day 1, there was no statistically significant difference between the time that the experimental subjects spent in a quadrant of the large restraining pen corresponding to the table quadrant containing the stimulus brood of three ducklings or any of the three empty quadrants ($p > 0.0083$). On Day 2, however, the stimulus brood of three ducklings was preferred significantly more than the empty quadrant to the right ($F(1, 15) = 22.514, p < 0.0083$). The stimulus brood of three ducklings was not preferred significantly more than the empty quadrant to the left of the stimulus brood ($F(1, 15) = 8.263, p > 0.0083$) or to the empty quadrant opposite to the stimulus brood ($F(1, 15) = 9.251, p > 0.0083$). It should be noted that the preference for the brood of three ducklings compared to the empty quadrant opposite to the brood of three ducklings approached statistical significance ($F(1, 15) = 9.251, p = 0.008$). From Day 3 to Day 7 the stimulus brood of three ducklings was preferred significantly more than the three empty quadrants ($p < 0.0083$). There were no

statistically significant differences among the preferences exhibited for the three empty quadrants ($p > 0.0083$) on Days 3 to 7.

Discussion

Several conclusions can be drawn from the results of this experiment. First, it was determined that the criterion for determining the location of the entire brood (the table quadrant in which seven out of the 10 ducklings occupied) was a simple and easy-to-measure unit of observation. The use of this criterion was further facilitated by the generally synchronous movements of the experimental brood. Second, videotaping the trials proved to be unnecessary for recording the location of the brood and was deemed to be unnecessary in Experiments 2, 3, and 4. Third, the extremely low latency scores of the experimental brood on Days 2 to 7, and the brood's overwhelming preference for the stimulus brood of three ducklings over the majority of this experiment, suggests that the stimulus objects were biologically appropriate.

These results suggest that the stimulus brood of three ducklings is very attractive to a larger brood of 10 ducklings at least from Day 3 through Day 7. The finding on Day 2 that the brood of three ducklings was close to being preferred to a statistically significant degree over a preference for the quadrant opposite to the brood of three ducklings, may suggest that these results would have been statistically significant given a larger sample size. The next two experiments will use larger sample sizes for statistical purposes. Experiment 2 examined whether the brood of three ducklings was unique in attracting the larger experimental brood of 10.

**EXPERIMENT 2: IS AN EXPERIMENTAL BROOD OF 10 DUCKLINGS
ATTRACTED TO A SMALLER STIMULUS BROOD OF THREE DUCKLINGS
OR A STIMULUS BROOD SIMILAR IN SIZE TO THE
EXPERIMENTAL BROOD?**

Individual ducklings show an attraction to broods but, when given a choice, prefer the largest brood available to them (Bruce & Shapiro, 1977a). The largest brood in Experiment 1 was the experimental brood. It was hypothesized, however, that the attraction between brood members of the largest brood, i.e., the experimental brood, would not preclude an attraction to another, unfamiliar, brood of ducklings.

This experiment examined whether or not the attraction of the experimental brood to the stimulus brood of three ducklings in Experiment 1 was unique or was due to the absence of a more attractive stimulus. Smith and Shapiro (1975) found that when a previously preferred brood of nine (the largest brood in the experiment) was made to be the smallest brood, larger broods were preferred by single ducklings significantly more than the previously preferred brood of nine ducklings or an empty quadrant. The current experiment employed similar methodology. A larger stimulus brood of nine ducklings was pitted against a stimulus brood of three ducklings, the brood preferred in Experiment 1. Since a duckling in the experimental brood of 10 sees nine other members in its brood, this situation presumably equated the experimental brood with the stimulus brood of nine ducklings. In this experiment, eight experimental broods of 10 ducklings each were tested for their preferences for a smaller brood of three ducklings, a brood of nine ducklings, or two empty quadrants for 15 min a day for seven days.

Hypotheses

Experiment 1 used a new methodology that involved testing the preferences of a brood of ducklings. Since it was unknown if the procedure would be successful, all possible pairwise comparisons between quadrants were conducted to determine which quadrants were preferred. The procedure was effective and the results indicated that the preferences of a brood could be determined using this methodology and that the brood of 10 ducklings was attracted to the smaller brood of three ducklings. The success of the methodology used in Experiment 1 provided the rationale to test specific a priori hypotheses about the preferences of the broods being tested in Experiment 2. In the latter experiment, it was hypothesized that the experimental brood of 10 ducklings would prefer the stimulus brood of nine ducklings. In particular, this experiment tested three specific hypotheses:

- 1) The experimental brood of ten ducklings would prefer the stimulus brood of nine ducklings over the stimulus brood of three ducklings.
- 2) The experimental brood of ten ducklings would prefer the stimulus brood of nine ducklings over the empty quadrant to its left.
- 3) The experimental brood of ten ducklings would prefer the stimulus brood of nine ducklings over the empty quadrant to its right.

Experiment 1 tested six pairwise comparisons since an a priori hypothesis could not be supported by previous experiments. Because of the success of Experiment 1, only three pairwise comparisons were conducted in Experiment 2.

Methods

Subjects

Experimental subjects. The experimental subjects in this experiment were 96 mallard ducklings obtained and reared in the manner described in the General Methods section. Eight broods of 12 ducklings each were reared. This experiment was conducted over two weeks in order to obtain the number of ducklings required. Week of testing, therefore, became a between-subjects factor in this experiment. Four broods of 12 ducklings were reared each week. Ten ducklings from each brood were randomly selected for testing for 15 min each day for seven days. The remaining two ducklings in each brood served as spares. Testing eight broods a day is the minimum number of testing units usually used for statistical reasons. Since each brood served as a single testing unit, 96 ducklings were required for statistical analysis.

Stimulus objects. The stimulus objects were a total of 30 mallard ducklings obtained and reared communally in the same manner as described in the General Methods section. This experiment was conducted over two weeks in order to obtain the number of ducklings required and the between-subject factor of week-of-testing was included in the analysis for the same reason that was given for the experimental subjects. Fifteen ducklings were reared each week. Twelve of these ducklings were randomly selected on each day of testing to serve as the stimulus broods of three and nine used in this experiment. The remaining three ducklings served as spares.

Apparatus

The apparatus was the sand-covered table in the sound-deadened experimental chamber described in the General Methods section.

Procedure

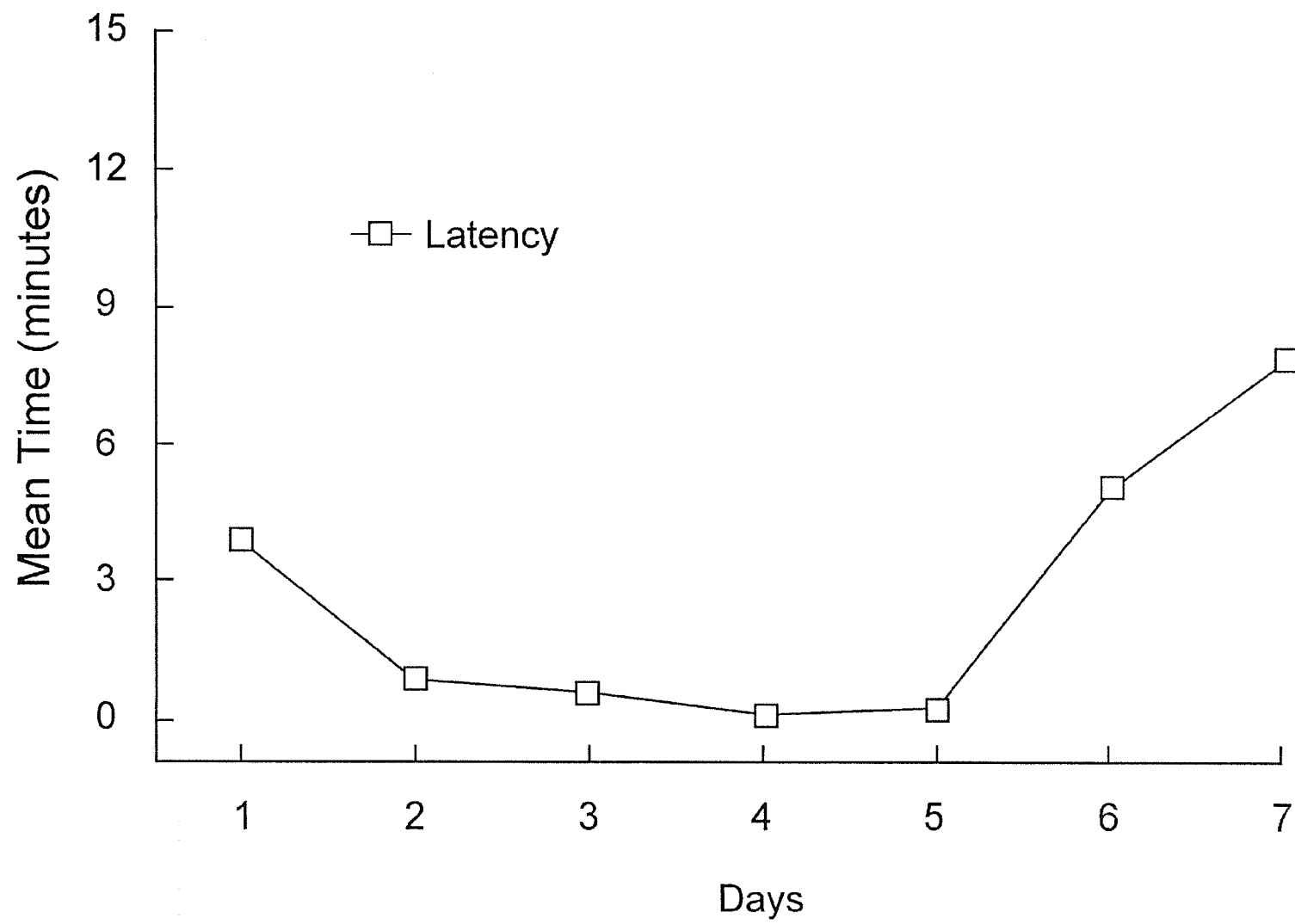
The table quadrant location of the brood of three ducklings was randomly determined. The brood of nine ducklings was placed in the corner cage of the table quadrant opposite to the brood of three ducklings. The stimulus objects remained in their respective table quadrants for the duration of each day of testing. The other two table quadrants remained empty. The first experimental brood on each day of testing was randomly placed in one of the empty quadrants within the large retaining pen in the centre of the sand-covered table corresponding to one of the two table quadrants not containing a stimulus brood. In subsequent trials, the experimental brood was placed into one of the two quadrants in an alternating manner such that an equal number of experimental broods began their trials in each of the two empty quadrants. The empty quadrant in the large retaining pen into which the experimental brood was placed had one brood to its left and one brood to its right. The sand in the large retaining pen was cleaned between trials. This experiment was conducted over two weeks in order to obtain the number of ducklings required.

Results

Figure 5 shows the latency time of the experimental brood. Latency decreased over the first two days much as it did in Experiment 1, although to a lesser degree. Declining latency times over the first two days of the experiment were also found in Experiment 1 and may be due to increased locomotion and a decrease in time spent sleeping as the ducklings matured. In contrast to Experiment 1, however, latency times increased dramatically over Days 6 and 7 of this experiment. The mean amount of time

Figure Caption

Figure 5. Mean time the experimental broods took to make a choice among quadrants in Experiment 2.



the experimental broods spent in each of the quadrants over the seven days is illustrated in Figure 6.

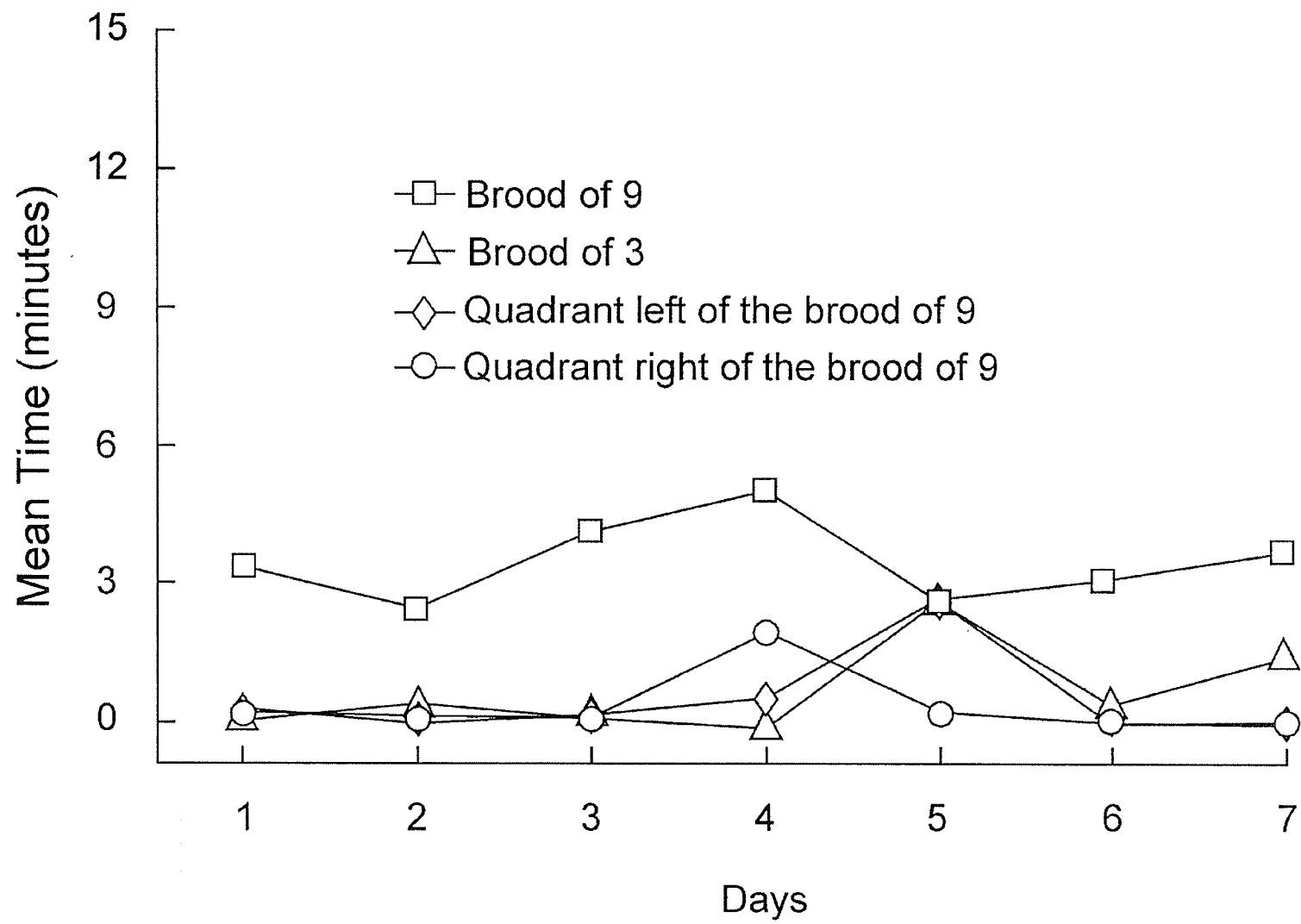
A three-way analysis of variance with a repeated measures design on two factors (stimulus objects and days) and a between subjects design on one factor (week-of-testing) was used to analyze the data. Because the experiment was conducted over two weeks, the between-subjects factor of week-of-testing was analyzed to determine if the data from each week could be combined. There was a statistically significant main effect for weeks ($F(1, 6) = 7.025, p = 0.038, \text{partial } \eta^2 = 0.539$), meaning that the behaviour of the subjects differed significantly between Week 1 and Week 2 in Experiment 2.

The statistically significant effect for week-of-testing was unexpected. There are many reasons to assume that this finding is an anomaly. First of all, the ducklings were only hatched a week apart so seasonal variation should not be a factor. The ducklings from each week were derived from the same flock so variation from that source should be minimal. Standard operating procedures involving incubation, hatching, and rearing practices were used and further reduce variability between hatches. In addition, a week-of-testing effect was not found in Experiment 1, nor has it been encountered during the last 30 years of research in the Avian Behaviour Laboratory. The effect could be due to random error associated with a relatively small sample size.

The estimated marginal means from each week were examined to determine the cause of the difference between weeks. The estimated marginal means refers to the mean times the experimental broods spent in each quadrant and the 95% confidence interval in which the values fall. Examination of the estimated marginal means suggests that the effect was due to a statistically significant difference between Week 1 and Week 2 in the

Figure Caption

Figure 6. Experiment 2: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing the stimulus brood of nine, the stimulus brood of three, and two empty quadrants.



mean time the experimental broods spent with the stimulus objects on Day 6. On Day 6, in Week 2, the experimental broods spent significantly more time in all of the quadrants than they did on Day 6 in Week 1.

The magnitude of the effect size for week was 0.539, which is considered to be large according to Cohen (1988) but is not necessarily applicable to this research design. This particular effect size is small relative to others obtained in this series of experiments (for example, the effect size calculated for the combined data for stimulus objects is 0.826). A smaller effect size for this main effect means that the effect for week-of-testing accounts for a relatively smaller amount of the variability observed. Because the effect was due only to a difference in means between replications on Day 6 and had a relatively moderate effect overall, the data from both replications were combined and a two-way analysis of variance on the combined data was performed. If the data from both weeks were not combined, and the data from each week were analysed individually, each week would only have had a sample size of four.

The two-way analysis of variance with repeated measures on two factors (stimulus objects and days) revealed a main effect for stimulus objects ($F(3, 18) = 28.399, p < 0.001$, partial $\eta^2 = 0.826$). There was no main effect for days ($F(6, 36) = 1.330, p = 2.69$, partial $\eta^2 = 0.181$) and there was no interaction effect between days and stimulus objects ($F(18, 108) = 0.611, p = 0.884$, partial $\eta^2 = 0.092$).

Because three a priori hypotheses were made predicting that the stimulus brood of nine ducklings would be preferred over the stimulus brood of three ducklings, the empty quadrant to its left, and the empty quadrant to its right, three pairwise comparisons were conducted in order to determine if the stimulus brood of nine was preferred to the

stimulus brood of three ducklings and the two empty quadrants. Because three pairwise comparisons were made, each comparison used an alpha of 0.017 ($\alpha = 0.05/3$) for the same reasons that were stated in Experiment 1 (p. 75). The brood of nine ducklings was preferred significantly over the brood of three ducklings ($F(1, 6) = 25.194, p = 0.002$, partial $\eta^2 = 0.808$), the empty quadrant to the left of the brood of nine ($F(1, 6) = 49.996, p = 0.000$, partial $\eta^2 = 0.893$), and the empty quadrant to the right of the brood of nine ($F(1, 6) = 35.199, p = 0.001$, partial $\eta^2 = 0.854$) over the seven day testing period.

Discussion

The experimental broods preferred the stimulus brood of nine ducklings over the stimulus brood of three ducklings, the preferred brood in Experiment 1, and the two empty quadrants. This finding suggests that the preference of the experimental broods for the stimulus brood of three ducklings in Experiment 1 may be due to the fact that the stimulus brood of three was the only stimulus available and that larger broods of ducklings, when given the choice, are attracted to the larger of two broods as is suggested by Experiment 2. This experiment shows that ducklings in a broods are attracted to the largest brood available to it, which is in line with research investigating the preferences of individual ducklings.

Although Experiment 2 supported the prediction that the experimental brood would prefer largest brood available, this preference was not as strong as the preference of the experimental broods for the stimulus brood of three in Experiment 1. There are some important differences between Experiments 1 and 2.

Duckling behaviour. Duckling behaviour during the trials was variable but some generalizations can be made. Trials usually started with the experimental broods orienting toward the stimulus broods after the lights were turned on in the experimental chamber. The experimental broods would sometimes move as a loosely-knit group to one of the table quadrants that contained one of the two stimulus broods briefly before spreading out in a random fashion over the sand-covered table and engaging in investigative behaviours, in particular, pecking sand, droppings, and the wire cage. Preening behaviours were also observed during and after these periods of investigative behaviour. The trials often began with an active period in which the ducklings were engaged in investigative or preening behaviour followed by a period of relative inactivity. The majority of time that seven or more ducklings spent together in any one quadrant in the large retaining pen was during the ducklings' inactive periods.

The effect of presenting two broods. Experiments 1 and 2 were different in several respects, most notably, the difference in latency times and the reduced time spent by the experimental broods in any quadrant in Experiment 2 in comparison to Experiment 1. The differences between the two experiments seem to be a result of simultaneously presenting two stimulus broods to the experimental broods in Experiment 2. The experimental broods in Experiment 2 spent a much smaller proportion of each 15-min trial in any of the table quadrants containing a stimulus brood in comparison to Experiment 1. The broods may have spent less time in any quadrant because the stimulus broods and the experimental broods were in close proximity to each other. Because the experimental broods were between each of the stimulus broods, and so close to them, this situation may have had the effect of creating one very large brood. The experimental

broods were, essentially, in the centre of this very large brood. Because of this location, the experimental broods may not have approached either of the stimulus broods.

The behaviour of the stimulus objects may also support the notion that the centre of the apparatus, i.e. being in the centre of this very large brood, is the ideal place for the ducklings to be. Behavioural observations indicated that the stimulus broods attempted to reach the experimental broods by poking their heads through the wire cages far more often than the experimental broods ever tried to reach the stimulus objects. Despite the fact that the centre of a brood may be the warmest and safest place for a duckling to be, the experimental broods, which were essentially in the centre of this very large brood, still showed a preference for the stimulus brood of nine ducklings.

The effect of two broods on latency. The presentation of two stimulus broods may also have had an effect on latency. It was expected that the experimental brood would quickly make a choice for the stimulus brood of nine ducklings. This prediction was based on the low latency times of the experimental brood in Experiment 1. In that experiment, the experimental broods very quickly approached the only stimulus brood available to it, sometimes moving towards the vocalizations of the stimulus broods in the dark before the trial had even commenced. In Experiment 2, however, when the experimental broods were presented with the stimulus broods (which were placed in opposite corners of the experimental apparatus, with the experimental brood between them), they did not approach the stimulus broods as quickly as expected.

There were some similarities and some differences between Experiment 2 (see Figure 5, p. 86) and Experiment 1 (see Figure 3, p. 74). First of all, both experiments started with higher latencies that decreased over the first two days. This was attributed to

an overall increase in motor activity as well as a proportional decrease in time spent sleeping as the ducklings matured. Latencies in both experiments were low on Days 3 to 5 but greatly increased on Days 6 and 7 in Experiment 2, during which time the amount the ducklings slept increased.

There may be several reasons for the increasing latency over the final two days of Experiment 2. One reason may be that the ducklings were habituating to the experimental apparatus. It may be that the experimental broods were learning that the testing environment did not pose an immediate threat to their well-being, which may have decreased their attraction to other ducklings for the benefits that they could provide such as protection and warmth, and subsequently slowed their reaction time during these trials on Days 6 and 7 (i.e. increased their latency times). This result is a possibility in repeated measures studies in which the same subjects are tested every day. The solution to the problem would be to use a between-subjects study in which eight new experimental broods are tested every day. Such a large number of ducklings would require that this experiment be run over several weeks in order to obtain a sufficient number of ducklings.

The increase in latency over the last two days did not manifest itself in Experiment 1. Habituation would have been far more likely in Experiment 1 because the experimental broods were tested eight times each day for seven days rather than just once a day for seven days as was done in Experiment 2. Habituation may be part of the reason, however, for why the ducklings became less likely to explore the experimental apparatus and more likely to just sleep through the last two days of Experiment 2.

The second possible reason for the increase in latency on Days 6 and 7 may be physiological changes in the ducklings. As ducklings mature, they are less dependent upon other ducklings or a brooding mother for heat. Perhaps the experimental brood was less attracted to the stimulus broods as a source of heat. This possibility is also unlikely given the fact that the temperature of the experimental chamber was controlled and was the same as the temperature in the brooding units. On Days 6 and 7 of Experiment 2, the ducklings were not huddled as close to each other as they were during the trials earlier in the week. On Days 6 and 7 in Experiment 1, however, the ducklings were huddled very close together, suggesting that even though they were less reliant upon their broodmates for heat, they still maintained a great deal of contact.

Another possible physiological change is that the ducklings were growing and simply getting larger. Also, as the ducklings grew, the space between the ducklings decreased. The growing ducklings may, therefore, have perceived themselves as being closer to the stimulus broods than they did during the first five days of the experiment, with the result that they were not motivated to make a choice to approach either stimulus brood. The experimental broods' "comfort zone" may have increased over the last two days of the experiment which may have led to their taking longer to make a choice between stimulus objects/quadrants.

The effect of two broods on variability. The presentation of two stimulus broods may also have had an effect on the variability seen between trials and week of testing of this experiment. In comparison to Experiment 1, the experimental broods in Experiment 2 spent much less time in any table quadrant that contained a stimulus brood. Variability in latency was seen in this experiment far more than in Experiment 1. In Experiment 2 the

ducklings would generally move into a table quadrant shortly after the trial began and would then spread out over the table quadrants. This finding relates to the fact that low latency scores did not always translate into longer times spent in a table quadrant containing a stimulus brood. In several instances, if the ducklings did not make a choice immediately, they had latency scores that spanned the 15-min testing session because fewer than seven ducklings would enter a single table quadrant at the same time. It is also possible that the variability observed was due to the use of a small sample size. It is likely that testing more broods would significantly decrease variability between trials and between weeks. The use of more subjects and the elimination of variability may also eliminate the statistically significant interaction effect that was found in this experiment. The number of broods used in Experiment 2, however, was still sufficient to show a fairly strong preference for the larger of the two stimulus broods.

The results of this experiment were very interesting. The presentation of the two stimulus broods on opposite sides of the experimental broods seems to have had the unforeseen effect of creating a "comfort zone" for the experimental broods. Because the experimental broods were, in effect, in the centre of a what was essentially a large brood due to proximity of the stimulus broods to the experimental broods, it is believed that they spent less time near any of the stimulus objects overall and were slower to make a choice between stimulus objects. In retrospect, this outcome should not be surprising when one considers the importance of the brood and the benefits ducklings would obtain from being in the centre of a very large brood. Despite being in the centre of this very large brood, however, the experimental broods still preferred, to a statistically significant extent, the stimulus brood of nine over the brood of three and the two empty quadrants.

Implications of Experiment 2. The results of Experiment 2 had ramifications for the next planned experiment in this study. The planned study involved the presentation of a total of three stimulus broods to the testing situation. Adding yet another brood, however, may exacerbate the problem encountered in Experiment 2. Therefore, before the planned experiment was conducted, Experiment 2 was replicated in a larger apparatus in an attempt to increase the distance between the experimental broods and the stimulus broods as well as the distance between the stimulus broods themselves. The purpose of this experiment was to see if increasing these distances would take the stimulus broods out of the experimental broods' hypothesized "comfort zone", thereby increasing the length of time the experimental broods spent near the stimulus brood of nine as well as decreasing the latencies of the experimental broods.

EXPERIMENT 3: REPLICATION OF EXPERIMENT 2 USING A LARGER APPARATUS

This experiment replicated Experiment 2 using a larger apparatus to increase the distance between the experimental broods and the stimulus broods and the distance between the stimulus broods themselves. Eight experimental broods of 10 ducklings each were tested for 15 min each day for seven days for their preferences for a stimulus brood of three, a brood of nine, or two empty quadrants, in an enlarged testing apparatus. It was assumed that the ducklings would prefer the largest brood available to them as they did in the previous experiment. It was also assumed that the experimental broods would spend more time in close proximity to the largest stimulus brood and that the broods would

make this choice much faster than they did in the previous experiment, resulting in lower latency scores in this experiment.

Hypotheses

Experiment 3 tested the same three a priori hypotheses that were tested in Experiment 2. Specifically, these were:

- 1) The experimental brood of ten ducklings would prefer the stimulus brood of nine ducklings over the stimulus brood of three ducklings.
- 2) The experimental brood of ten ducklings would prefer the stimulus brood of nine ducklings over the empty quadrant to its left.
- 3) The experimental brood of ten ducklings would prefer the stimulus brood of nine ducklings over the empty quadrant to its right.

Because three a priori hypotheses were made, three pairwise comparisons were conducted to determine whether or not the stimulus brood of nine ducklings was preferred over the stimulus brood of three ducklings and the three empty quadrants.

Methods

Subjects

Experimental subjects. The experimental subjects in this experiment were 86 mallard ducklings obtained and reared in the manner described in the General Methods section. This experiment was conducted over two weeks in order to obtain the number of ducklings required. Therefore, week of testing became a between-subjects factor in this experiment. Forty-six ducklings were reared during the first week in two broods of 12 ducklings and two broods of 11 ducklings. Forty ducklings were reared during the second week in four broods of 10 ducklings. Ten ducklings were randomly selected for testing

on each day in Week 1. The ducklings not being tested were used as spares. Because duckling mortality was so low in the previous experiments, and because the large number of ducklings could not be obtained, fewer spares were used in Week 2.

Stimulus objects. The stimulus objects were a total of 28 mallard ducklings obtained and reared communally in the same manner as described in the General Methods section. Twelve ducklings were reared during the first week of this experiment and 16 ducklings were reared in the second week. During each week the stimulus objects were reared together in a single brood unit. Twelve of these ducklings were randomly selected on each day of testing to serve as the stimulus broods of three and nine used in this experiment. Any remaining ducklings served as spares.

Apparatus

The apparatus was similar to the sand-covered table in the sound-deadened experimental chamber described in the General Methods section except that the dimensions of the table were increased from 1.5 x 1.5 m to 2.4 x 2.4 m and built to encompass the actual dimensions of the interior of the experimental chamber. Only the dimensions of the experimental table changed. All other aspects of the apparatus, including the dimensions of the corner cages and the retaining pen, remained the same. This change resulted in an increase in the table surface area from 2.25 m² to 5.76 m², an increase in area by a factor of 2.56. The diagonal distance between corner cages increased from 1.14 m to 2.41 m (+1.27 m). The distance between the experimental broods' retaining pen and the stimulus broods' corner cages increased from 0.12 m to 0.76 m (+0.64 m). The distance between adjacently placed corner cages increased from 0.7 m to 1.6 m (+0.9 m). The resized apparatus is depicted in Figure 7.

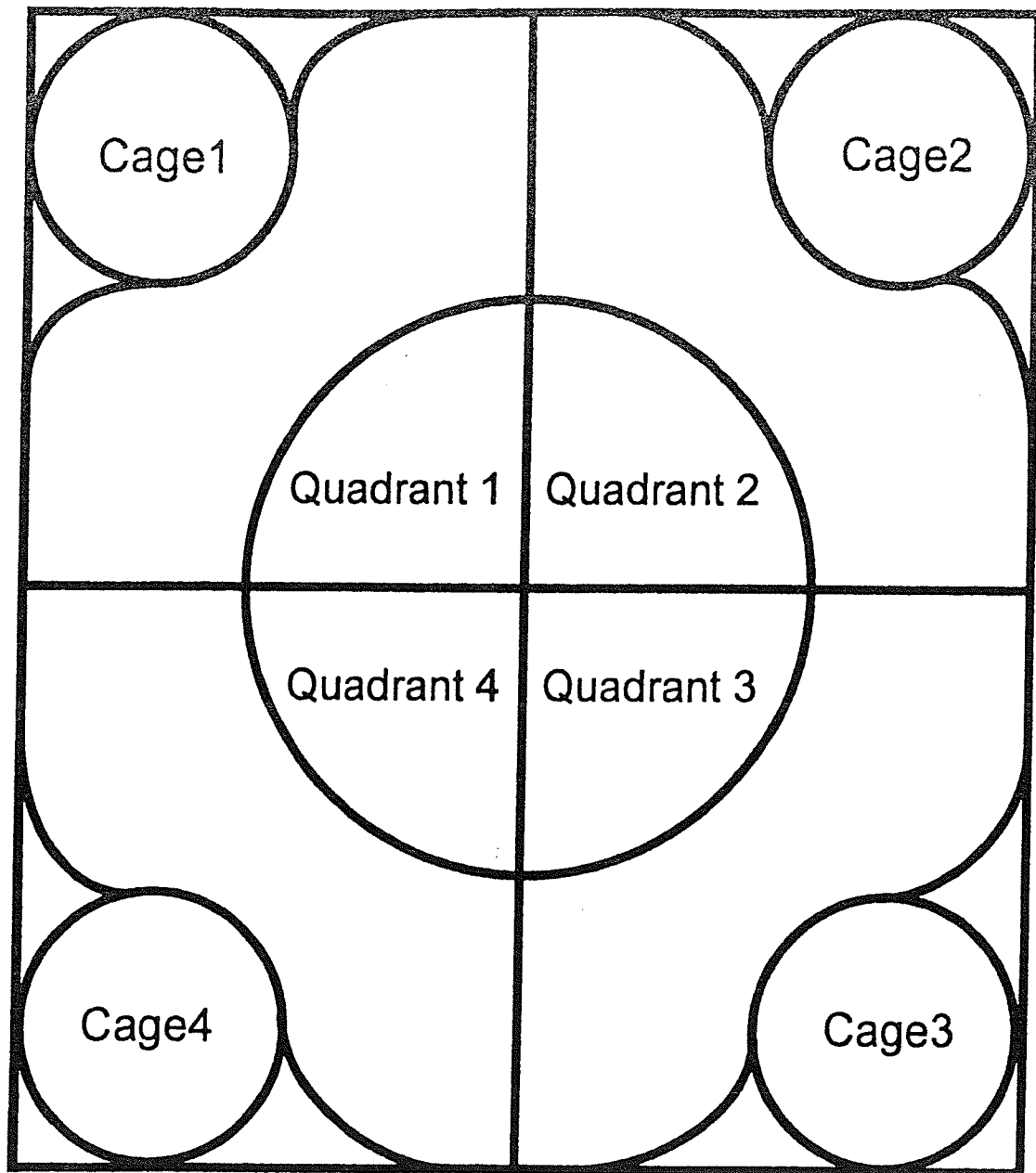


Figure 7. Overhead view of the enlarged experimental platform. This diagram is not drawn to scale. It is used to illustrate the increase in the distance between the experimental broods and the stimulus broods. Only the dimensions of the table changed. The dimensions of the corner cages and the retaining pen remained the same.

Procedure

The procedure used in this experiment was identical to that described in the previous experiment. Because the larger apparatus was built to the dimensions of the chamber, and because the larger apparatus remained at the same height above the floor as the smaller apparatus, the experimenter could only reach the experimental brood by stepping directly onto the surface of the experimental table. Footprints were smoothed out of the sand before every trial. Smoothing the sand took only a few seconds and did not greatly increase the time involved in placing the experimental broods in the chamber at the start of each trial. The sand within the large retaining pen was sifted of wastes after every trial.

Results

The mean latency time of the broods in Experiment 3 is illustrated in Figure 8. Since latency was expected to decrease in Experiment 3 in comparison to Experiment 2, the mean latencies of the broods in these two experiments were compared. The mean latency times from both Experiment 2 and Experiment 3 are illustrated in Figure 9. A two-way analysis of variance with a repeated measures design on one factor (days) and a between subjects design on one factor (week-of-testing) was used to analyze the data. Mauchly's test of sphericity revealed a statistically significant violation of the assumption of sphericity on the factor of days (Mauchly's $W(1, 20) = 0.006, p = 0.000$). Because the analysis significantly violated the assumption of sphericity, the Geisser-Greenhouse correction was used. This analysis revealed a main effect for days ($F(2.818, 39.449) = 6.605, p = 0.001, \eta^2 = 0.321$) but there was no interaction effect between days and experiment ($F(2.818, 39.449) = 1.074, p = 0.369, \eta^2 = 0.071$). There was no significant

Figure Caption

Figure 8. Mean time the experimental broods took to make a choice among quadrants in Experiment 3.

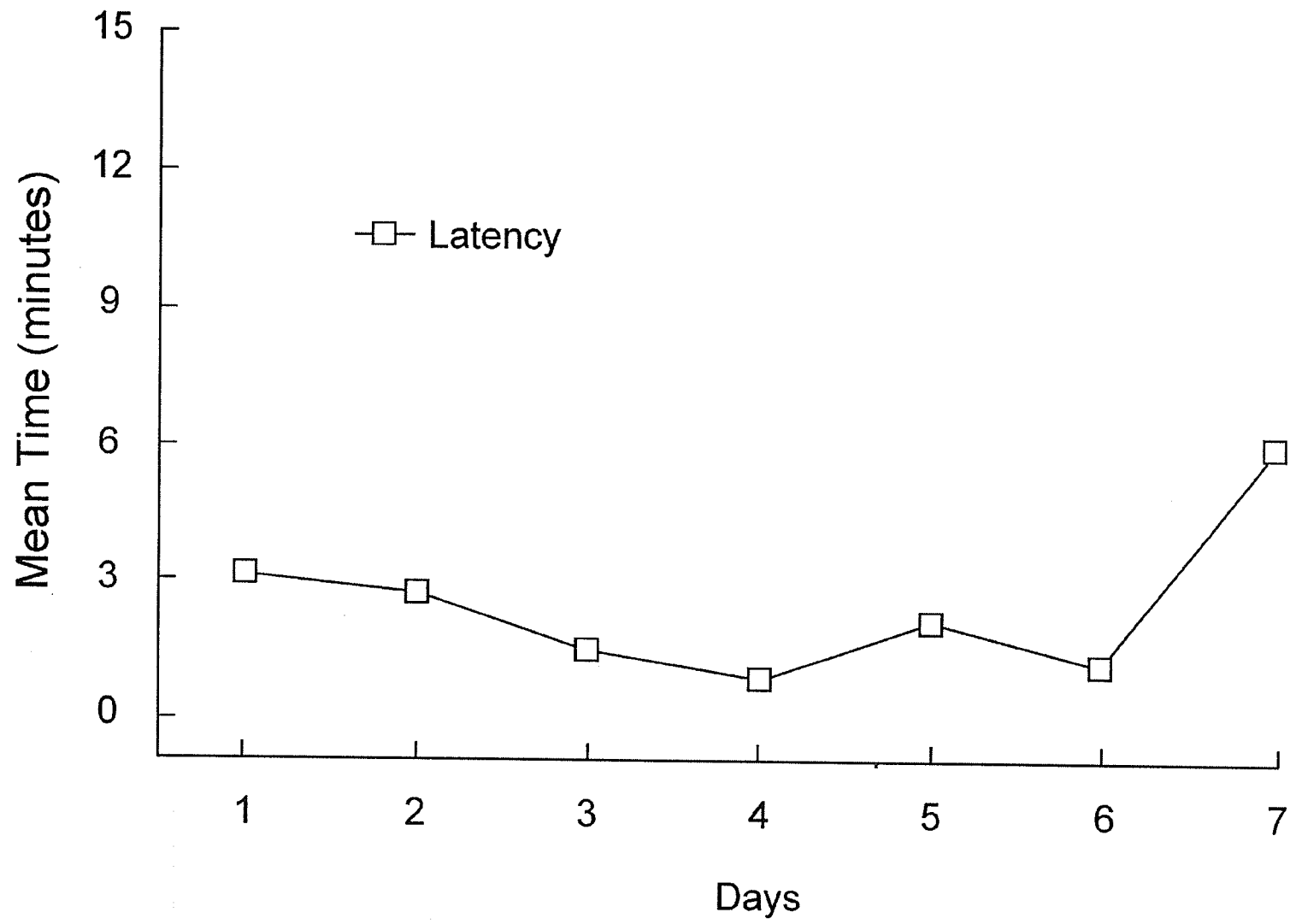
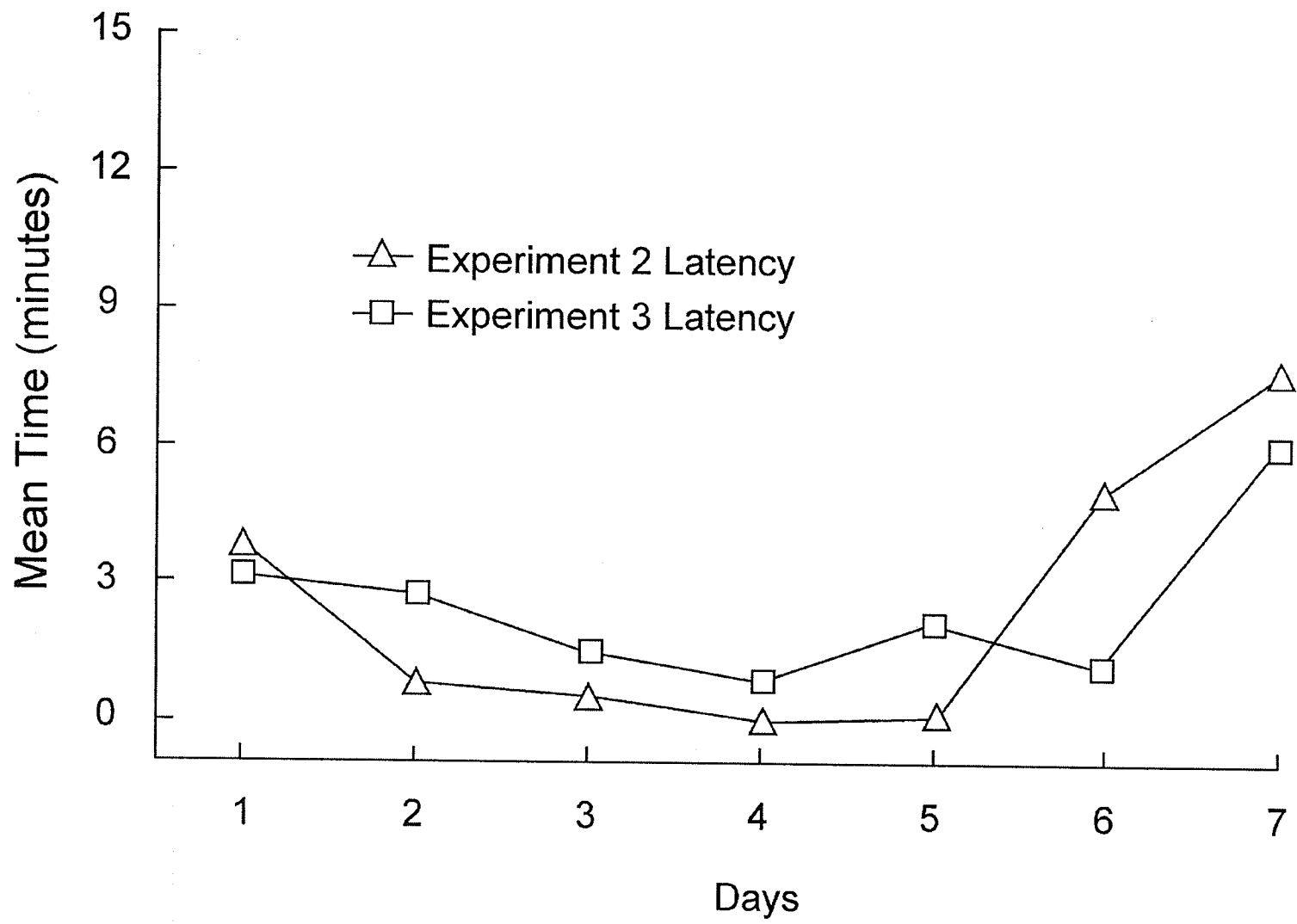


Figure Caption

Figure 9. Mean time the experimental broods took to make a choice among quadrants in Experiments 2 and 3.



difference between the latency times in Experiment 2 and Experiment 3 ($F(1, 14) = 0.001, p = 0.979, \eta^2 < 0.001$).

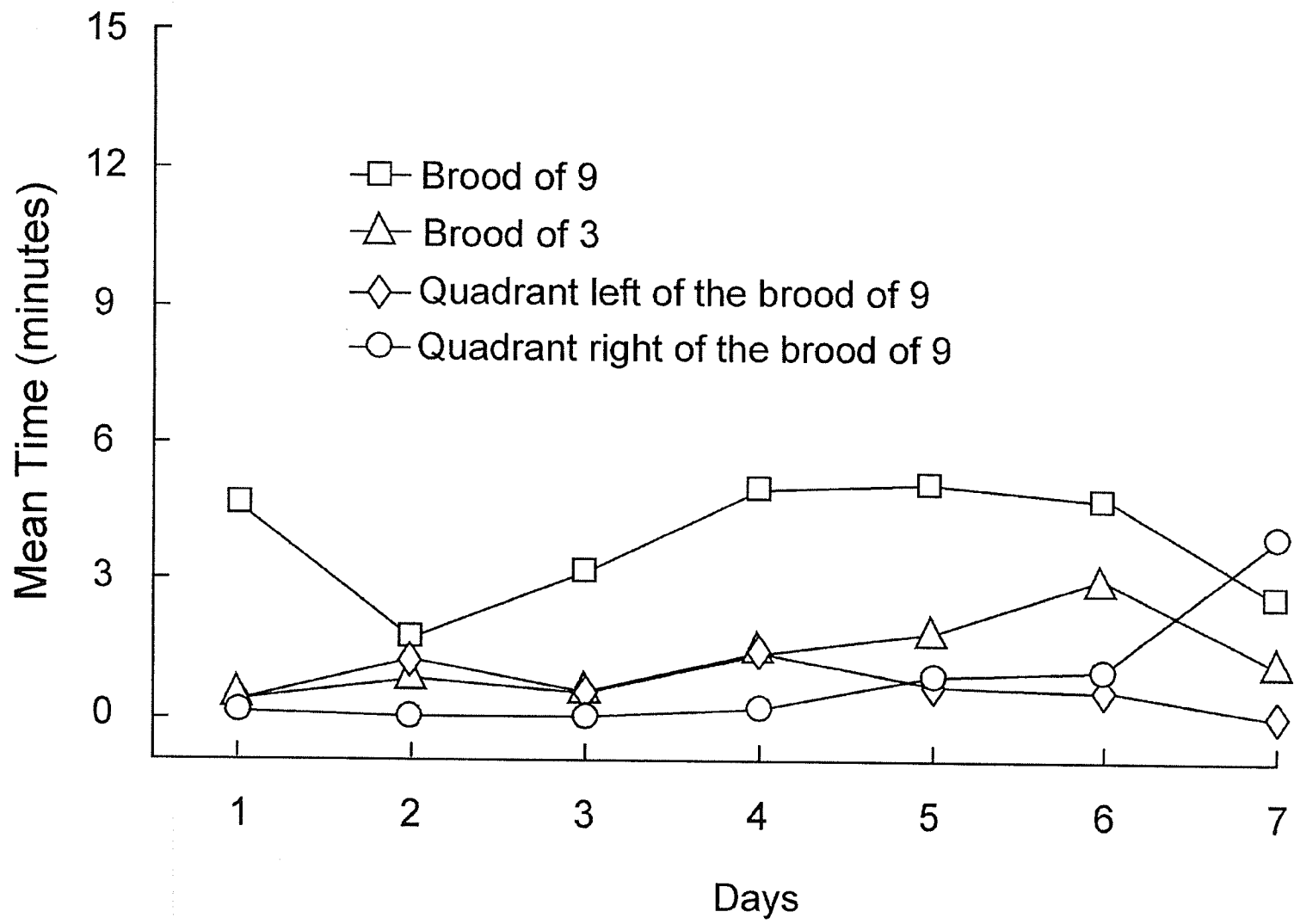
The mean time the experimental broods spent in each quadrant on each of the seven days is illustrated in Figure 10. A three-way analysis of variance with a repeated measures design on two factors (stimulus objects and days) and a between subjects design on one factor (week-of-testing) was used to analyze the data. There was a main effect for weeks-of-testing ($F(1,6) = 6.648, p = 0.042, \eta^2 = 0.526$) and a main effect for stimulus objects ($F(3,18) = 8.255, p = 0.001, \eta^2 = 0.579$). There was no main effect for days ($F(3,18) = 2.134, p = 0.073, \eta^2 = 0.262$).

As in Experiment 2, a statistically significant effect for weeks was found. Again, the source of this effect is unknown. The ducklings in Experiment 3 behaved very much like the ducklings in Experiment 2. The experimental broods took longer to make a choice between quadrants, and spent a great amount of time sitting between quadrants. The effect of the hypothesized "comfort zone" referred to in Experiment 2 may have led to an ambiguity in the preferences of the ducklings. This ambiguity, compounded with the small sample size, may have resulted in an increased variability between weeks.

To examine the source of the main effect for week-of-testing, the estimated marginal means from each week were examined to determine the cause of the difference between weeks. The estimated marginal means refers to the mean times the experimental broods spent in each quadrant and the 95% confidence interval in which the values fall. Examination of the estimated marginal means suggests that the effect, in a manner similar to that found in Experiment 2, was due to a difference between Week 1 and Week 2 in

Figure Caption

Figure 10. Experiment 3: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing the stimulus brood of nine, the stimulus brood of three, and two empty quadrants.



the mean time the experimental broods spent in any of the quadrants on Day 5. Again, for the same reasons outlined in Experiment 2, it was considered an anomaly even though it occurred again. This phenomenon did not occur in Experiments 1 or 4 in this series, and since Experiment 3 was a replication of Experiment 2, the results were considered to be a function of this particular testing situation. The reason why this occurred needs to be elucidated in future research.

Power refers to the ability to detect a treatment effect. The greater the power, the more likely treatment effects will be detected. To attain the appropriate power to examine the preferences of the ducklings, the data from each week had to be combined. Because the main effect for week-of-testing was only due to a difference in the total amount of time the experimental broods spent in the quadrants on Day 5, and for all the reasons to combine the data outlined in Experiment 2, the data from both weeks of this experiment were combined and a two-way analysis of variance with repeated measures on two factors (stimulus broods and days) was run on the data.

A two-way analysis of variance with repeated measures on two factors (stimulus objects and days) revealed a main effect for stimulus objects ($F(3,18) = 8.255, p = 0.001$, partial $\eta^2 = 0.579$). There was no main effect for days ($F(3,18) = 2.134, p = 0.073$, partial $\eta^2 = 0.262$) nor was there an interaction effect between stimulus objects and days ($F(3,18) = 8.255, p = 0.572$, partial $\eta^2 = 0.131$).

Three pairwise comparisons were made at $\alpha = 0.017$ to test the three a priori hypotheses in a manner similar to that of Experiment 2. The brood of nine ducklings was not preferred significantly over the brood of three ducklings ($F(1, 6) = 6.059, p = 0.49$, partial $\eta^2 = 0.502$). The brood of nine ducklings was preferred significantly over the

empty quadrant to the left of the brood of nine ($F(1, 6) = 17.177, p = 0.006$, partial $\eta^2 = 0.741$), and to the empty quadrant to the right of the brood of nine ($F(1, 6) = 10.845, p = 0.017$, partial $\eta^2 = 0.644$).

Discussion

Although the brood of nine was preferred more than the brood of three, and despite that the graph is very similar to that of Experiment 2, it was not preferred to a statistically significant extent. Increasing the size of the apparatus did not have the expected effect of increasing the time the experimental broods spent in any of the quadrants. There could be numerous reasons for this finding. One reason may be that increasing the distance between stimulus broods has no effect on the preferences of the experimental broods and that there is no “comfort zone” around the experimental broods or that the limits of this “comfort zone” are very great.

Although the creation of a “comfort zone” is a possibility, the position of the experimental broods might be the integral factor in not finding a preference for the brood of nine ducklings. The position of the experimental broods was not changed in this experiment i.e. they were still located between the stimulus brood of three and the stimulus brood of nine ducklings. Because they were still between the stimulus broods and because there were limits to the size the table could be increased, the distances involved in this experiment may not have been effective in eliciting a stronger response from the experimental broods for the brood of nine ducklings.

Another, related, possibility could be that confining the experimental broods to a retaining pen in the centre of the apparatus that was the same size as that used in Experiment 2 kept the experimental broods an equal distance from either stimulus brood

and thus made the stimulus broods more difficult for the experimental broods to discriminate between. For example, approaching either stimulus brood would not increase the experimental broods' proximity to or distance from either of the stimulus broods to any significant degree. All of these possibilities deserve examining but represent a series of experiments that are beyond the scope of this particular study.

Since the larger apparatus did not have the predicted effect on the experimental broods' preferences or latencies, the final planned experiment was conducted using the original apparatus. Since the perceived size of the experimental brood and the actual size of the stimulus brood of nine were equated in the previous two experiments, the final experiment examined whether the stimulus brood of nine was preferred because it was similar in perceived size to the experimental brood or whether a brood larger than itself will be more attractive, and thus, preferred.

EXPERIMENT 4—IS A BROOD ATTRACTED TO A LARGER BROOD?

This experiment was conducted to determine whether or not a brood larger than the experimental broods would be preferred more than the previously preferred broods of three and nine ducklings. Eight experimental broods of 10 ducklings each were tested for 15 min each day for seven days for their preferences for stimulus broods of three, nine, or 17 ducklings, as well as an empty quadrant.

Hypotheses

In Experiment 4 it was hypothesized that the experimental brood of 10 ducklings would prefer the largest stimulus brood available to them just as individual ducklings have in the past (Shapiro & Bruce, 1977a). In particular, this experiment tested three specific hypotheses:

1. The experimental brood of ten ducklings would prefer the stimulus brood of 17 ducklings over the stimulus brood of nine ducklings.
2. The experimental brood of ten ducklings would prefer the stimulus brood of 17 ducklings over the stimulus brood of three ducklings.
3. The experimental brood of ten ducklings would prefer the stimulus brood of 17 ducklings over the empty quadrant.

Because Experiment 4 tested these specific hypotheses, only three pairwise comparisons were conducted to determine if the stimulus brood of 17 was preferred over the other stimulus broods and the empty quadrants.

Methods

Subjects

Experimental subjects. The experimental subjects in this experiment were 80 mallard ducklings obtained and reared in the manner described in the General Methods section. Ducklings were reared in broods of 10 rather than 12 because the large number of subjects needed for this experiment could not be obtained. The experiment was conducted over two weeks in order to obtain the number of subjects required. Therefore, week of testing became a between-subjects factor in this experiment. Five broods of 10 ducklings were reared during the first week of the experiment and three broods of 10

ducklings were reared during the second week of the experiment. Also, during the second week of the experiment, a brood of dark coloured ducklings was reared as an experimental brood. Dark-downed ducklings had to be used in this experiment because too few ducklings of normal colouration were hatched. It was decided that the data derived from the dark-downed experimental brood would be compared to the data from the other experimental broods. If the behaviour of this brood was not any different from the other experimental broods, it would be included in the overall analysis. It should be noted that these darker ducklings are wild mallard ducklings that are expressing a phenotype for dark-coloured down. No behavioural abnormalities were expected.

Stimulus objects. The stimulus objects were 70 mallard ducklings obtained in the same manner described in the General Methods section. A total of 34 ducklings were reared during the first week of the experiment and 36 ducklings were reared during the second week of the experiment. A minimum of 29 ducklings was required each week to comprise the broods of three, nine, and 17 ducklings in this experiment. It was decided that the stimulus objects should all be of the same colouration so as not to introduce this possibly confounding variable into the testing situation. The extra ducklings reared during each week were used as spares for both the stimulus broods and, if required, as spares for the experimental broods. During each week, the ducklings were reared communally in approximately equal numbers in two brood units. On each day of testing, three, nine, and 17 ducklings were randomly chosen to serve as the stimulus broods in the experiment.

Apparatus

The apparatus was the original sand-covered table in the sound-deadened experimental chamber described in the General Methods section.

Procedure

The location of the stimulus broods of three, nine, and 17 ducklings was randomly determined. The remaining quadrant was empty. The experimental brood was placed onto the sand-covered table within the large retaining pen in the centre of the apparatus in the one remaining table quadrant not associated with a stimulus brood. The sand within the large retaining pen was cleaned and smoothed after every trial.

Results

Figure 11 depicts the mean latencies of the experimental broods over the seven days of Experiment 4. Latency remained relatively low and constant over the entire seven days. Low latency scores indicate that the subjects were healthy and that they were responding to biologically appropriate stimulus objects. The mean amount of time the experimental broods spent in each of the quadrants over the seven days is illustrated in Figure 12.

A three-way analysis of variance with a repeated measures design on two factors (stimulus objects and days) and a between subjects design on one factor (week-of-testing) was used on the data. This analysis was conducted on all eight broods of ducklings. The analysis revealed no significant main effect between weeks in this experiment ($F(1, 6) = 3.668, p = 0.104, \eta^2 = 0.379$). Since there was no significant difference between the preferences of the ducklings in each week of the experiment, the data from each week

Figure Caption

Figure 11. Mean time the experimental broods took to make a choice among quadrants in Experiment 4.

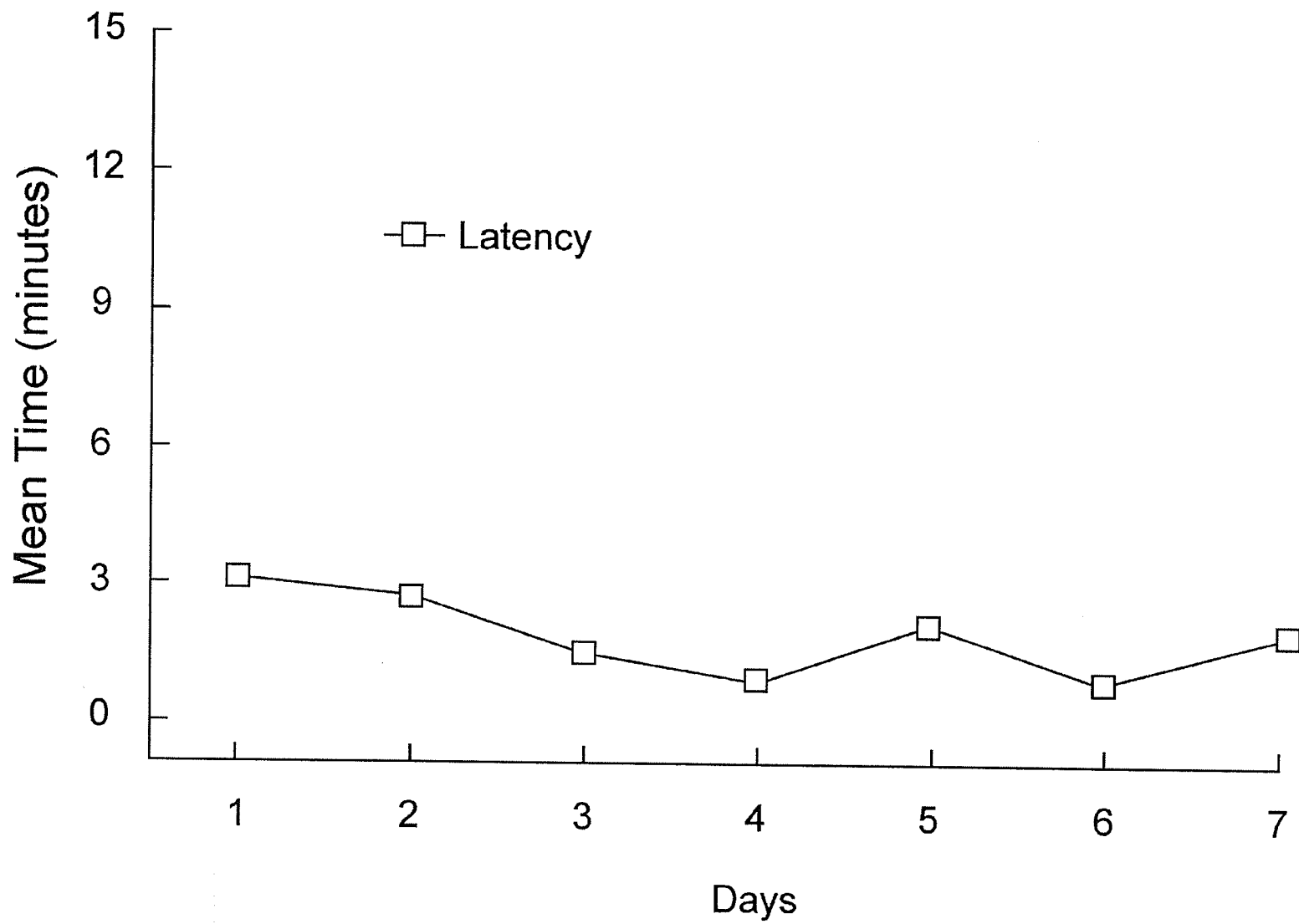
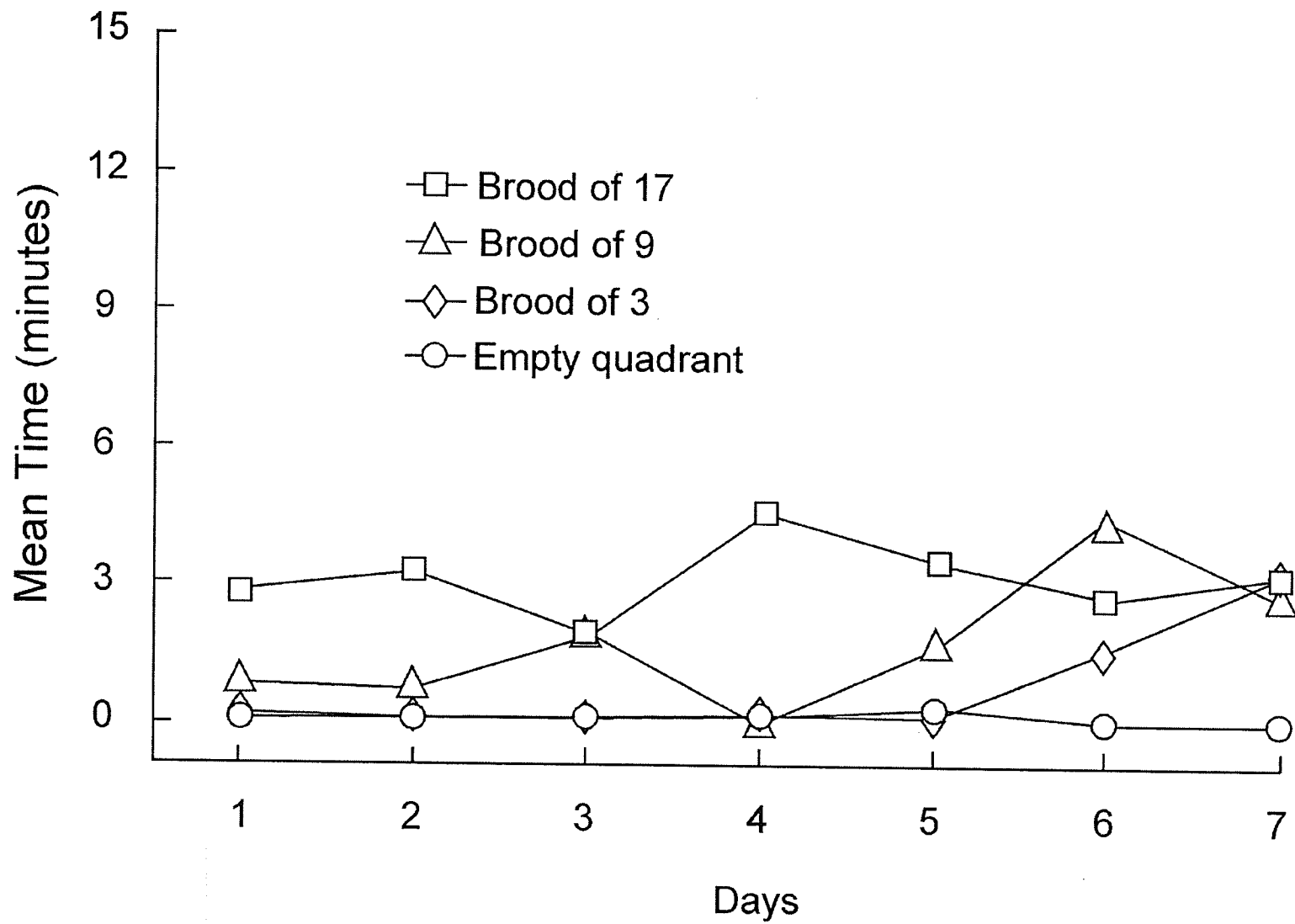


Figure Caption

Figure 12. Experiment 4: Mean time the experimental brood spent in a quadrant of the large retaining pen corresponding to the table quadrant containing a stimulus brood of three, nine, or 17 ducklings, or an empty quadrant.



were combined and a two-way analysis with repeated measures on two factors (stimulus objects and days) was used to analyze the data.

A two-way analysis with repeated measures on two factors (stimulus objects and days) was used to analyze the data. It found a main effect for stimulus objects ($F(3, 18) = 8.375, p = 0.001$, partial $\eta^2 = 0.583$). There was no main effect for days ($F(6, 36) = 2.028, p = 0.087$, partial $\eta^2 = 0.253$) nor was there an interaction effect ($F(18, 108) = 0.790, p = 0.708$, partial $\eta^2 = 0.116$).

Although behavioural differences between the normal-coloured broods and the dark-coloured brood were not expected, another three-way analysis of variance with repeated measures on two factors (stimulus objects and days) and a between subjects on Week-of-testing was run on the data obtained from the seven normal-coloured broods. This analysis excluded the data from the one dark-coloured brood. This analysis was conducted to determine if the data from the one dark-coloured brood added a significant amount of variability to overall results. The results were the same as the results obtained from the three-way analysis using all eight broods. There was no statistically significant effect for week-of-testing ($F(1, 5) = 2.23, p = 0.196$, partial $\eta^2 = 0.308$), nor was there an effect for days ($F(6, 30) = 1.208, p = 0.329$, partial $\eta^2 = 0.195$) or an interaction effect ($F(18, 90) = 1.649, p = 0.064$, partial $\eta^2 = 0.248$). There was a statistically significant effect for stimulus objects ($F(3, 15) = 5.391, p = 0.010$, partial $\eta^2 = 0.519$). Since the data from the one dark-coloured brood did not add a significant amount of variability to the overall data, the results of the original three-way analysis were used.

To determine the source of the main effect for stimulus objects, and to determine whether or not the brood of 17 was preferred significantly more than the other stimulus broods and the empty quadrant, three pairwise comparisons ($\alpha = 0.017$) between the brood of 17 and the broods of nine and three and the empty quadrant were performed on the data from all eight experimental broods. The main effect for stimulus objects appears to be due to a preference for the brood of 17 over the empty quadrant ($F(1, 6) = 30.421, p = 0.001, \eta^2 = 0.835$). The brood of 17 was preferred over the brood of nine ducklings and the brood of three ducklings. It was not, however, preferred to a statistically significant extent over the brood of nine ($F(1, 6) = 4.063, p = 0.090, \eta^2 = 0.404$), nor was it preferred to a statistically significant extent over the brood of three ($F(1, 6) = 6.799, p = 0.040, \eta^2 = 0.531$).

In one of the trials in this experiment an unusually small duckling from the stimulus brood of 17 was able to squeeze through the wire mesh of its retaining cage and approached the experimental brood in the centre of the apparatus. The experimenter paused the trial, which stopped the 15-min trial and turned the lights off in the chamber. He then placed the duckling back into its retaining cage and placed an already cut piece of wire mesh along the inside of the cage to prevent the duckling from escaping again. This whole process took less approximately a minute and did not seem to affect the behaviour of any of the ducklings on the apparatus.

Discussion

The brood of 17 ducklings was preferred but it was not preferred significantly more than other stimulus broods, and was only preferred significantly over the empty quadrant. The effect of having another brood surrounding the experimental broods may

have had the effect of creating an even larger brood in which the experimental broods found themselves located in the middle. The experimental broods, surrounded by even more ducklings in this situation, did not exhibit a clear preference for any brood. The brood of 17 was only preferred significantly over the empty quadrant. It was not preferred to a statistically significant degree from the broods of three and nine ducklings.

Another factor that may have compounded the problem of having too many ducklings surrounding the experimental brood may lie in the fact that on some days of the experiment, the broods of nine and 17 were adjacent to each other. This situation occurred on Days 2, 3 and 6. The brood of 17 was somewhat preferred on Day 2, the broods of 17 and nine were preferred approximately the same on Day 3, and the brood of nine was somewhat preferred on Day 6. It was observed that on these days the experimental brood would often be situated immediately between these two broods leading the ducklings to overlap both quadrants. Movement of the experimental brood while they were huddling together could have led to seven out of 10 ducklings entering one of the quadrants. Time spent in any quadrant during these instances may not be reflective of any actual choice made by the brood itself and may just be due to the random movements of the brood. This problem was not encountered in the previous experiments that utilized two stimulus broods because they were placed immediately opposite to each other. The locations of the stimulus broods in this experiment were randomly determined. Placing the two largest broods opposite to one another may have led to a clearer preference for the brood of 17. Although the placement of the stimulus broods may have had an affect on preferences, it seems unlikely that placing the two largest broods opposite to each other would have affected overall preferences to a

significant degree in this experiment. For example, on days when they were opposite to each other, it did not seem to affect the preferences of the experimental broods.

It is believed that no preference for the brood of 17 was found because of the testing situation. In comparison to the experimental broods in Experiments 2 and 3, these broods seemed to be even more comfortable in the centre of what they may have perceived as a very large brood. Although the graph in Figure 12 suggests that more time was spent with the brood of 17 over the first five days of the experiment, this preference was not statistically significant.

GENERAL DISCUSSION

The preference of individual ducklings for other broods of ducklings, especially larger broods, is well known (Lorenz, 1935/1957, Rogan & Shapiro, 1974; Shapiro & Bruce, 1977b). In the natural environment, ducklings are part of a brood. The preferences of broods of ducklings have not been studied. The purpose of this series of experiments was to examine the preferences of an entire brood of ducklings. Investigating the preferences of a brood of ducklings provides a better understanding of avian attachment behaviour as it develops and is expressed in a more common situation in the natural environment i.e. in the context of a brood.

Experiment 1 had two purposes. The first purpose was to develop a methodology to test the preferences of a brood. The second purpose was to test the preferences of broods of 10 ducklings for a smaller stimulus brood of three ducklings or for no stimulus. An existing apparatus from the Avian Behaviour Laboratory in the Psychology Department at the University of Manitoba that was built to test the preferences of

individual ducklings was modified to accommodate the testing of an entire brood. This apparatus consisted of a sand-covered square table. Lines were drawn in the sand such that the table was divided into four quadrants. A large retaining pen that overlapped all four quadrants was placed in the centre of the apparatus. The experimental broods of ducklings were placed within this large retaining pen. A cage in each corner of the table was used to contain the stimulus broods. These cages were referred to as corner cages. The time the experimental broods spent in each table quadrant within the large retaining pen was recorded. Time spent by the experimental broods in each table quadrant was regarded as an indication of a preference for the stimulus in that quadrant.

The location of individually tested ducklings is easy to measure and record using a focal-animal method of observation. In this series of experiments, the experimental broods consisted of 10 ducklings. Since a focal-animal method of observation was impossible using this many subjects, a new criterion for determining the location of the brood had to be formed. The location of the brood was arbitrarily determined to be the quadrant that contained seven out of the 10 ducklings making up the brood. This criterion was chosen as the cut-off because it was felt to be representative of the preferences of the larger portion of the brood used. Because ducklings in the natural environment rarely wander away from the brood, it was probable that the ducklings would tend to move synchronously between table quadrants within the large retaining pen. It was also felt that this criterion would be sufficiently robust to account for the occasional slow or wandering duckling. A focal-animal-like method of testing could again be employed and applied to the brood. Data could be recorded in a manner similar to that used when testing individual ducklings.

Experiment 1 found that the experimental brood of 10 ducklings overwhelmingly preferred the stimulus brood of three ducklings to any of the three empty quadrants. The amount of time the experimental broods spent within the retaining cage in the table quadrant that contained the stimulus brood of three ducklings was low for the first two days of the experiment but increased over last five days of this experiment. Latency times were correspondingly high during the first two days and low for the rest of the experiment. Ordinarily, high latency scores would indicate sick subjects or the presence of biologically inappropriate stimulus objects. In this case, however, this pattern seemed to be due to the fact that the ducklings spent more time sleeping during the first two days of the experiment and, consequently, were slow to move towards any quadrant. By the third day, however, the experimental broods had matured to the point that they moved towards the stimulus brood of three ducklings quickly and, consequently, had low latency times. They then spent the majority of each trial in the table quadrant of the retaining pen corresponding to the table quadrant containing the brood of three ducklings, where they would either preen or sleep together in a huddle.

Experiment 1 was successful in that the simple modification to an existing testing apparatus and the new criterion for determining the location of the brood of ducklings was effective in determining the preferences of a brood of ducklings. Also, the finding that a large brood of ducklings was attracted to a smaller brood of ducklings provided an interesting question. Would the stimulus brood of three ducklings be preferred by the experimental broods if a larger brood was also available to it? Past experiments testing individual ducklings have found that larger broods are preferred (Rogan & Shapiro, 1972, 1974; Bruce & Shapiro, 1977a, b). Experiment 2 was conducted to determine if

experimental broods would prefer a stimulus brood that was equal in size to them (larger than the brood of three ducklings but not larger than the experimental broods themselves) or the stimulus brood of three ducklings.

Experiment 2 found that the experimental broods significantly preferred the stimulus brood of nine ducklings, the brood equal in perceived size to each experimental brood, over the stimulus brood of three ducklings or the two empty quadrants. Even though the stimulus brood of nine was preferred, the time the ducklings spent in any one quadrant was much less than in Experiment 1. As in Experiment 1, the ducklings were slow in making a choice between quadrants during the first two days of the experiment. In contrast to Experiment 1, however, latency increased over the last two days of the experiment. Overall, the ducklings took longer to make a choice between quadrants and spent less time overall in any quadrant. Often the ducklings were spread out investigating the retaining pen such that fewer than seven ducklings were in any one of the quadrants.

The difference between the latency results and the stimulus object preferences obtained in Experiment 1 and the same results obtained in Experiment 2 was felt to be due to a limitation of the testing apparatus. It seemed that the experimental broods, in Experiment 2, in the centre of the apparatus, were "comfortable" in their position between the stimulus broods. Being surrounded by two other broods may have led to the creation of a "comfort zone".

A "comfort zone" was postulated because of the notable difference in latency times of the experimental broods in Experiments 1 and 2 and the amount of time the experimental broods spent near the stimulus broods in the same two experiments. In Experiment 1, the experimental broods spent almost all of their time near the stimulus

brood of three ducklings. In Experiment 2, the experimental broods spent a great deal of time moving between quadrants. The experimental broods in the centre of the apparatus exhibited a great deal of investigative behaviour and engaged in comfort movements all over their retaining pen. Consequently, less time was spent in any of the retaining pen quadrants overall. It may have been the case that the ducklings making up the experimental brood were so near both of the stimulus objects that they did not prefer either brood. Having two broods of ducklings so close to the experimental broods in the middle of the apparatus may have created the effect of having one very large brood. If the ideal location in a brood is the centre of the brood, i.e. the location where the greatest amount of protection and warmth could be derived, the experimental broods may have been "comfortable" in their position and the preference for the larger of the two stimulus broods was not as strong in comparison to Experiment 1. Despite the creation of a "comfort zone", however, the experimental broods still preferred the stimulus brood of nine ducklings significantly more than the previously preferred stimulus brood of three and the two empty quadrants in Experiment 1.

In an attempt to reduce the effect of this "comfort zone", Experiment 2 was replicated using a larger apparatus. It was thought that increasing the distance between the stimulus broods in their corner cages and increasing the distance between the experimental brood in their retaining pen and the stimulus broods would reduce the effect of the "comfort zone". It was thought that under these conditions the experimental broods would spend more time near the stimulus brood of nine ducklings and would reduce their latencies as well. Experiment 3 found that the stimulus brood of nine ducklings was preferred like it was in Experiment 2 (although this preference fell short of statistical

significance), but increasing the size of the apparatus, at least to the dimensions that it was increased to in this experiment, did not reduce the effect of this "comfort zone". The ducklings still spent less time in any of the quadrants in comparison to Experiment 1. Increasing the dimensions of the apparatus did not decrease the latencies of the experimental broods to any significant degree either. Since the larger apparatus did not have the expected effect, a fourth experiment was conducted in the original apparatus.

Experiment 4 was conducted to determine if the experimental broods would prefer a stimulus brood larger than itself. A brood of 17 ducklings was pitted against the previously preferred broods from the first two experiments, a stimulus brood of three and a stimulus brood of nine ducklings. The experimental broods did not significantly prefer the larger stimulus brood of 17 over the stimulus broods of nine and three ducklings. The stimulus brood of 17 was only preferred significantly more than the empty quadrant. Although the experimental broods spent more time near the stimulus brood of 17 ducklings than the other broods, this preference was not statistically significant. The effect of the hypothesized "comfort zone" may have been enhanced by adding another, even larger, brood to the testing situation. It may have masked the potential strength of a preference for the larger stimulus brood of 17.

Behaviour of the stimulus broods

The behaviour of the stimulus broods is important to the interpretation of the results of these experiments. Overall, there did not seem to be any particular behaviour that was effective in attracting the experimental broods to the stimulus broods. In fact, it seemed that the experimental broods were by far the most attractive of any of the broods in these experiments. Behavioural observations made during testing indicated that the

stimulus broods attempted to reach the experimental broods far more than the experimental broods tried to reach the stimulus broods. Behavioural observations also indicated that the smallest stimulus brood, the brood of three, seemed to put the most effort, overall, into "attempting" to reach the experimental brood. The larger stimulus broods attempted to reach the experimental broods much less often.

It is very interesting that some of the ducklings in the stimulus brood of 17, in Experiment 4, still "attempted" to reach the experimental broods. These ducklings "attempted" to reach the experimental broods despite the fact that they were already embedded in the largest brood. In one instance, which necessitated a simple modification of the stimulus broods' retaining cage, an unusually small duckling from the stimulus brood of 17 actually fit through the wire retaining cage and approached the experimental brood of 10, necessitating the experimenter to stop/pause the trial and place the duckling back into its retaining cage.

The attraction of the brood of 17 ducklings to the experimental broods further supports the finding that larger broods are preferred. In all of the experiments, the stimulus broods were usually positioned in their retaining cages as close as possible to the experimental broods. The stimulus broods may have been attracted to behavioural cues from the experimental broods. The experimental in the centre of the apparatus seemed to be in a "comfort zone" in-between the stimulus broods. The behaviour of the experimental broods in this "comfort zone" was characterized by a great deal of investigative and preening behaviours. Perhaps these behaviours were attractive to the stimulus broods. Further, the attraction to the experimental broods may not be an attraction to the broods themselves but may be an attraction to the physical location of the

experimental broods. A common behaviour associated with the stimulus broods during the trials was a duckling's tendency, when huddling with its brood, to shuffle towards the centre of the brood. This desire to be in the centre of the brood may also apply to the "large brood" that was created in the testing situation. The stimulus broods in the corner cages attempted to reach the centre of this large brood where, it is presumed, the greatest amount of warmth and safety would be derived. It is also important to note that these ducklings "attempted" to leave their own brood in order to join the broods of unfamiliar ducklings in the centre of the apparatus.

Distress vocalizations

Considering the number of attempts many ducklings in the stimulus broods made to reach the experimental broods, they seldom appeared to be in much distress. Despite many attempts to squeeze through the wire mesh of the retaining cages, the stimulus broods emitted very few distress vocalizations. Of any of the broods, the stimulus brood of three was the most likely to distress vocalize. These occurrences were more frequent in the first experiment than in the later experiments and may be due to stress associated with the increased handling of the stimulus brood in that experiment. The most likely reason for more distress vocalizing in Experiment 1, however, may be due to the fact that there were fewer ducklings being used in that experiment. Both the stimulus brood of three ducklings, which were handled after every trial, and the experimental broods which were not handled after each trial, seemed much more anxious as evidenced by their distress vocalizations in the testing situation in comparison to other experiments in which more than one stimulus brood was present.

When distress vocalizations occurred, however, they were often ineffectual in attracting the attention of the experimental brood. The only time that distress vocalizations elicited any kind of approach response from the experimental broods was during periods in which the experimental broods were themselves distress vocalizing. The experimental brood was most responsive to the vocalizations of the stimulus brood of three in-between trials in Experiment 1 when, with the experimental brood still present, but in the dark, the location of the stimulus brood was changed. When the lights again turned on in the chamber for the next trial, the experimental brood, which was sometimes distress vocalizing, usually had already started moving toward the distress vocalizing stimulus brood in the dark, and would often run toward it as soon as visual confirmation of their location was made.

Improving the methodology

This series of experiments represents a promising methodology for testing the preferences of a brood of ducklings. The results also suggest that several aspects of the methodology need to be addressed. One improvement that has already been suggested is the placement of the stimulus broods. When using three stimulus broods, the two largest broods should be placed opposite to one another so that the experimental broods have to make a clear choice between the largest broods and will not congregate between the table quadrants housing them. The latter situation may result in no clear preference for either one of the broods.

Considering the absence of statistically significant results when three stimulus broods were presented, perhaps no more than two broods should be used in this apparatus. In this series of experiments, time spent in each quadrant decreased and

latency increased as the number of stimulus broods increased and suggests an increased ambivalence of the experimental broods toward any of the stimulus broods. This ambivalence was attributed to the increased "comfort" of being surrounded by ducklings. The stimulus broods may have been in such close proximity to the experimental broods that the latter were not motivated to move toward any one of them.

Increasing the distance between the stimulus broods and, supposedly, increasing the motivation of the experimental broods, should be attempted once again. Although increasing the distance between the broods was ineffective in Experiment 3, the apparatus may still have been too small. The size of the enlarged table was confined by the size of the experimental chamber. A larger table built in a larger experimental chamber would be needed to investigate this possibility. Alternatively, the experiment could be performed in a more semi-natural environment where there are no restraints on the size of the testing apparatus being used.

Another suggestion would be to test eight new broods of ducklings every day in a between-subjects design. In this experimental design, the potentially confounding effect of habituating to the testing situation can be controlled. Again, this design would require an extremely high number of ducklings (eight new subject broods of 10 ducklings a day for seven days = 560 ducklings per experiment). It was also suggested, however, that habituation to the testing situation would have been more likely in Experiment 1, in which the same broods were tested eight times a day for seven days rather than just once a day. These ducklings did not seem to show a decreasing preference for the stimulus brood over time.

In the ideal situation, all of the trials should be conducted in the same week. This results in fewer ducklings being used because only one group of stimulus ducklings will need to be reared. Conducting all the trials at once would also possibly eliminate any seasonal variation between hatches and would lead to better experimental control overall. Seasonal effects were minimized in the current experiments by conducting the experiments over two consecutive weeks.

Future Research

The methodology used in these experiments represents a starting point for several follow-up studies. For example, as stated earlier, the size of the apparatus can be increased to an even greater extent than it was in Experiment 3. Similarly, the size of the retaining cage of the experimental broods can be manipulated to determine if an increased ability to approach a stimulus brood affects preferences. Another line of experiments can manipulate the size of the experimental brood. The current series of experiments only tested broods of 10 ducklings. A very large range of experimental brood sizes can be tested to determine how preferences for other broods are affected by the size of the experimental broods themselves. These are just examples of what experiments can be conducted using this methodology. Considering that avian attachment research has only tested ducklings individually for decades, there are countless opportunities to repeat past research using the brood as its focus instead of just an individual duckling.

Why a larger brood?

So what is the attraction to a brood and, especially, a large brood? Evidence exists that being in a group may have a survival benefit to its members. One such benefit would be a defence from predators. For example, in line with the confusion effect hypothesis, the scattering of the brood during an attack may confuse a predator enough to increase the chances of the brood to escape (see Caro, 1986). Another anti-predator defence inherent in a group is the increased chance of predator detection. Members can share the role of predator detection, reducing individual vigilance and increasing the chances of predator detection. Studies show that as flock size increases, vigilance in female mallards and green-winged teals (*Anas crecca crecca*) decreases (Lendrem, 1983; Gauthier-Clerc, Tamisier, & Cezilly, 1998). Vigilance also decreases in males, but only after the post-breeding moult when they shed their bright conspicuous plumage and adopt their cryptic “eclipse” plumage (Lendrem, 1983). Decreases in individual vigilance in a group have also been found in other bird species, such as crested terns (*Sterna bergii*) (Roberts, 1995) and sanderlings (*Calidris alba*) (Roberts, 1997).

Hamilton (1971) suggests that members of a group use each other for cover in a strictly selfish desire for self-preservation. This “selfish-herd” hypothesis states that using other members of the group for cover increases the individual’s chance of surviving, and thus, increases their fitness. There is a tendency towards increasing group cohesiveness in the presence of a predator, which may afford the members of a group safety. Flocks of sanderlings increase their cohesiveness when disturbed by a predator (Roberts, 1997) and European wigeons (*Anas penelope*) form larger flocks the further they move away from the safety of water (Mayhew & Houston, 1989). Rodriguez, Andren, and Jansson (2001)

found that in several species of tit (*Parus cristatus*, *P. montanus*, *P. ater*, and *Regulus regulus*) group cohesion and flock size increased according to habitat-mediated predation risk. Large amalgamations of up to 150 ducks have been observed in cases of predator initiated alarm in Barrow's goldeneye and bufflehead (Munro & Bedard, 1977). Bruce and Shapiro (1977b) found that a duckling is attracted to the largest brood available to it, even if the brood is abnormally large to the point that it may be non-adaptive in the natural environment (i.e. a very large brood could become more conspicuous to a predator). For example, the increased level of noise emitted from more ducklings in a larger brood may attract a predator. However, if cover is what is attractive to a duckling, perhaps this is why a very large brood is preferred.

There are several more advantages to a brood. A brood can provide heat to its members. Ducklings can huddle together to keep warm in the absence of the mother. Contact comfort has been found to be important in infant primates (Harlow, 1958) and may also be important to ducklings. Real or surrogate-mothers in Harlow's experiments were preferred to wire-mesh mothers because of the contact comfort they provided. Perhaps this also occurs in ducklings, as evidenced by the cessation of a lone duckling's distress calls when it is reunited with another duckling (Collias & Collias, 1956).

A brood can also potentially provide itself with more food than an individual could on its own. Moore (1977) argues that membership in a flock affords a "strength in numbers," especially in species that must face interspecific competition in foraging activities. Though mallards may not have to compete for food with other species, feeding in a group still has benefits. In shallow water, mallards paddle the bottom mud churning up invertebrates (McKinney, 1969). The action of more feet paddling in the water in

close proximity could result in more food being brought up to the surface, disproportionate to the number of feeding individuals. Merganser hatchlings use a similar water-churning method on schools of fish (Beard, 1964). Despite the benefits of a brood, ducklings in some species do not necessarily have a higher survival rate in enlarged broods, namely, those duck species that form crèches. High mortality rates in crèches of the common eider are common (Gorman and Milne, 1972). However, in both these situations, mortality is lower when the young are adopted by another mother and her brood or join a crèche than if the duckling were left on its own.

Although preference for the largest brood did not reach statistical significance in every experiment of the current series, broods of ducklings appeared to be attracted to larger broods as opposed to smaller broods or broods equal in size to itself but not larger than itself. Testing the preferences of a brood would help shed light on the formation of attachments in ducklings. Shapiro (1977) stated "we may be able to unravel some of the mysteries of imprinting if we use live models in the more naturalistic setting and if we examine the complex, dyadic interaction between parent and offspring" (p. 857). These studies demonstrate the importance of siblings and peers and open up many possibilities for research.

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