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Age-Related Differences in the Prey-Dropping Behavior of Herring Gulls (Larus argentatus)

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AGE-RELATED DIFFERENCES IN THE PREY-DROPPING BEHAVIOR OF HERRING GULLS (*LARUS ARGENTATUS*)

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ABSTRACT

Several avian species are known to drop prey with hard exteriors from a height in order to smash the prey open and gain access to the food inside. Such a complex foraging behavior involving multiple steps and use of novel foraging methods borders on tool use and is a fertile area in which to study cognitive development of foraging skills. I observed a wintering population of herring gulls utilizing prey-dropping behavior to feed on wedge clams (*Rangia cuneata*) at Jamestown Island, VA.

Prior studies on age-related differences in foraging efficiency in birds have shown that young or inexperienced birds are less effective foragers than older conspecifics. I examined age-related differences in prey-dropping efficiency in herring gulls using plumage and soft-body part coloration to age gulls as first, second, third year or adult. I compared the variables of height of drop and size of prey dropped between these age classes to determine if there was a difference in foraging behavior.

I found no detectable differences in height of drop between any age classes of herring gull. All ages of herring gulls also dropped similar sizes of clams on average. However, yearling or naïve herring gulls dropped a broader size range of clams, including clams of low profitability in terms of caloric gain. I tested three hypotheses to determine why yearling gulls included these less profitable clams in their diets. Two of these hypotheses were focused on where yearlings were foraging for clams while the third looked at their ability to discriminate between different sizes of clams.

Yearling and experienced gulls differed with regard to prey size dropped due to lower prey discrimination abilities in the yearling gulls rather than yearlings foraging in poorer quality patches due to inexperience or exclusion by older gulls. Individual prey assessment skill is likely gained through trial-and-error learning after repeated drops of various sized clams. Implications for the development of prey-dropping behavior in general as well as directions of future research are discussed.

AGE-RELATED DIFFERENCES IN THE PREY-DROPPING BEHAVIOR OF HERRING GULLS (*LARUS ARGENTATUS*)

GENERAL INTRODUCTION

Many species of crows, gulls and raptors drop prey items in order to gain access to food that would otherwise be unavailable or difficult to consume (Cristol and Switzer 1999). Although there are some instances of softer-bodied prey being dropped, such as a rat or a spiny dogfish (Harber and Johns 1947, Cavanagh 1992), in general, birds drop prey with hard exterior coverings such as mollusks or nuts.

A typical avian prey drop involves a search period that ends when the prey item is obtained. The bird will then fly some distance with the prey to a hard surface such as a rocky beach or a road, ascend vertically and release the prey item from a particular height. This will result in the prey item being smashed open as a result of the impact, or remaining intact, in which case the bird will often repeat the drop until success is achieved. This typical series of steps for an avian prey drop is well described and well documented in gulls (Tinbergen 1960, Barash et al. 1975, Siegfried 1977, Beck 1980). Such foraging behavior that involves multiple steps, multiple decisions and the solving of novel problems is a fertile area in which to study the cognitive abilities of animals. Prey-dropping behavior in herring gulls (*Larus argentatus*), in particular, has been compared to tool use by non-human primates in terms of its cognitive complexity (Beck 1980). Age-related changes in foraging skill would suggest that learning and experience play a role in the efficiency with which these birds select and drop their prey. The herring gulls I observed, dropped only one prey type, the wedge clam (*Rangia cuneata*) at my study site on Jamestown Island, VA. The objective of my study was to determine if there were age-related differences in the execution of this complex foraging behavior for Jamestown Island herring gulls.

Study species

The herring gull is a common and familiar gull found in North America and Europe. North American herring gulls are year-round residents of the Great Lakes and much of the East Coast, including Virginia (Pierotti and Good 1994). Its winter range shows a strong association with open fresh or salt water with a fairly continuous distribution along all Atlantic, Pacific and Gulf coasts extending as far south as southern Central America. The herring gull is a generalist predator on pelagic and intertidal marine invertebrates, fishes, insects, and adults, eggs and young of other birds (Pierotti and Good 1994). It is also an opportunistic scavenger on fish, carrion, and human refuse with individual specialization on certain common prey types (Pierotti and Annett 1987, Pierotti and Good 1994). In mudflat microhabitats, foraging herring gulls commonly follow the retreating tide to capture worms and small bivalves. This is consistent with the foraging behavior I have observed on the mudflats at Jamestown Island, VA. Herring gulls there forage in the mudflats for wedge clams primarily during and before low tides when mud is either exposed or there is a very shallow ($\leq$ 2cm) layer of water covering the mud.

The herring gull is classified as a four-year gull, which means that it goes through a series of distinct molts throughout its early years and generally achieves definitive adult plumage when it is > 3 years old or during the fourth prebasic molt. Since all gulls are, in general, hatched and fledged within one month of each other during the summer, gulls born in a particular year are all approximately the same age. Therefore, the distinct plumages seen in herring gulls of different ages allow for rapid and fairly accurate aging of individuals in the field. The herring gulls feeding on wedge clams at Jamestown Island are doing so in the winter and had already achieved their basic plumage. Since basic plumages of first, second, third and adult birds are distinct, I was able to classify any bird that was seen for more than a few seconds. See Appendix A for a description of the charactistics of the four basic plumage types used for aging gulls in this study.

Avian prey dropping

Studies investigating avian species that drop hard-shelled prey items for food include birds of three different orders and have examined several aspects of this complex foraging behavior (Table 1). Several crow species have been studied in terms of their ability to drop hard-shelled prey efficiently. Carrion crows (*Corvus corone*) tended to choose the largest mussels and drop them on hard surfaces in order

TABLE 1

SOME PREVIOUS STUDIES ON PREY DROPPING SHOWING DIVERSITY OF PREY-DROPPING SPECIES, PREY DROPPED AND CONCLUSIONS.

Species	Prey	Conclusions	Reference
Corvus brachyrhynchos american crow	nuts – English and black walnuts	Crows optimize some aspects of dropping	Cristol and Switzer, 1999
Corvus caurinus northwestern crow	mollusk – whelks	Optimize drop height and prey size	Zach, 1978, 1979
Corvus caurinus northwestern crow	mollusk – clams	Optimize prey size	Richardson and Verbeek, 1986
Corvus corone cornix hooded crow	nuts	Changed dropping technique	Mienis, 1993
Corvus corone corone carrion crow	mollusk – mussles	Predictions of size, substrate and drop height preference	Whiteley et al., 1990
Haliaetus leucocephalus bald eagle	reptile – turtle	Bald eagles deliberately drop prey	Bindner, 1968
Larus argentatus herring gull	mollusk – clams eggs	Hardness of prey is dropping stimulus	Tinbergen, 1960
Larus argentatus herring gull	mollusk, crustacean, echinoderm	Dropping ability varies with age	Ingolfsson and Estrella, 1978
Larus argentatus herring gull	mollusk – clams	Prey dropping is cognitively complex	Beck, 1980
Larus argentatus herring gull	mollusk, crustacean, echinoderm	Prey selection varies depending on substrate	Kent, 1981
Larus argentatus herring gull	mullusk – mussels	Suggests observational learning	Conner, 1993
Larus delawarensis ring-billed gull	mollusk – mussels	Ring- billed gulls deliberately drop prey	Drennen, 1995
Larus dominicanus kelp gull	mollusk – mussel	Predict optimal drop height, actual height varies	Siegfried, 1977
Larus dominicanus kelp gull	mollusk – clams	Prediction of optimal prey size selection	Ward, 1991
Larus glaucescens glaucous-winged gull	mollusk	Hard substrates are preferred	Barash et al., 1975
Larus marinus great black-backed gull	mammal – rat	Mammal deliberately dropped by gull	Harber and Johns, 1947
Larus occidentalis western gull	mollusk – clams	Drop height varies with age	Maron, 1982

to minimize drop height (Whiteley et al. 1990). Northwestern crows (*Corvus caurinus*) dropped only the most profitable mollusks and did so from optimal heights (Zach 1979). American crows (*Corvus brachyrhynchos*) dropping walnuts adjusted the height of individual drops according to likelihood of theft, hardness of the walnut and the ground below, and the likelihood of the walnut breaking due to weakening from previous drops (Cristol and Switzer 1999). These studies all examined prey dropping behavior in the context of optimal foraging and suggest that various crow species maximize net energy gain during dropping behavior.

There have also been several studies on gull species that drop hard-shelled prey items, and these suggest that gulls are making optimal decisions with respect to height of drop, number of drops, choice of drop site and substrate or prey size selection (Barash et al. 1975, Siegfried 1977, Ingolfsson and Estrella 1978, Kent 1981, Maron 1982). Differences in the prey dropping ability of gulls with respect to age and experience have been addressed as well and suggest that younger gulls are less efficient than experienced adults. For example, glaucous-winged gulls (*Larus glaucescens*) showed an age-related progression of increased dropping efficiency with respect to substrate selection and drop height but not with choice of drop strategy (Barash et al. 1975). Juvenile kelp gulls (*Larus dominicanus*) were less successful than adults in smashing mussels open on the first drop attempt (Siegfried 1977). Juvenile western gulls (*Larus occidentalis*) were similarly less likely than adults to drop clams and dropped them from lower heights (Maron 1982). Yearling herring gulls were also less successful in smashing open clams, less efficient with respect to drop height and number of drops and less likely to drop clams than adults (Ingolfsson and Estrella 1978, Connor 1993). Previous studies of prey-dropping herring gulls have either been largely anecdotal or have not investigated prey size selection. Furthermore, these studies have not attempted to determine the underlying reasons for the apparent lower foraging efficiency of prey dropping juvenile herring gulls when compared to adults.

Acquisition of foraging skills in birds

An animal's behavior is shaped by natural selection to be efficient and successful so that energy waste is minimized. Foraging behaviors, which require a large number of decisions and large expenditures of energy often provide excellent examples of how natural selection can influence the efficiency of a behavior. If an animal does not achieve certain levels of efficiency, the energy and nutrition gained from their prey will not sufficiently offset the energy expended in obtaining and handling the prey. This is particularly evident in the complex foraging behavior of birds like herring gulls in which they drop hard-shelled prey items from the air to smash them open and gain access to the meat inside.

Juvenile birds in general employ different foraging strategies and forage less efficiently than adults. This difference in juvenile foraging is often the result of (1) immaturity of the beak, skeleto-muscular and neurological systems and (2) the time required to learn foraging skills (Marchetti and Price 1989). It has also been suggested that differences in foraging site selection, search methods, prey recognition and selection, prey capture ability, and food-handling time or technique could explain the lower foraging efficiencies of juvenile birds (Wunderle 1991). Examples are numerous: juvenile little egrets (*Egretta garzetta*) are less successful and less efficient than adults when searching for and capturing prey items (Cezilly and Boy 1988); capture rates and handling ability of young eurasian dippers (*Cinclus cinclus*) are less efficient than those of experienced adults (Yoerg 1994); winter feeding rates of snow buntings (*Plectrophenax nivalis*) show significant increases in efficiency with experience (Smith and Metcalfe 1994); young oystercatchers (*Haematopus ostralegus*) feeding on mussels go through a period of learning from their parents which can last over a year depending on the foraging strategy employed (Perez-Hurtado 1994).

Gulls show significant age-related differences in foraging efficiency when attempting kleptoparasitism either of conspecifics or other species (Burger and Gochfield 1981, Hesp and Barnard 1989, Amat and Aguilera 1990, Steele and Hockey 1995). In general, young gulls attempting kleptoparasitism are less successful than adults, are more likely to be targets of piracy attempts and are more likely to drop food when chased. Although young herring gulls kleptoparasitize less effectively than adults, yearling herring gulls do improve their foraging and piracy efficiency over time (Burger and Gochfield 1981). Herring gulls also show significant age-related improvement of foraging efficiency when feeding on starfish or refuse (Verbeek 1977, Greig et al. 1983). Lower overall feeding rates were seen in younger herring gulls despite using the experience of older conspecifics to choose where to forage. Young herring gulls feeding at garbage dumps had lower peck rates, took more paces per unit time and made more attempts to steal food or displace another bird from a feeding patch than adults. Although all ages of gulls displaced conspecifics from foraging patches with equal success, immature birds were less successful in obtaining food from a newly acquired foraging patch (Greig et al. 1983). These studies all attribute the lower foraging efficiency seen in juvenile birds to a required period of learning and improvement. In summary, juvenile birds or birds that are new to a particular foraging area or technique show decreased foraging efficiency when compared to adults or more experienced birds.

The concept of learning is often invoked to explain observed differences in foraging proficiency with age. However, to attempt to classify a given behavior as strictly learned or innate suggests the innaccurate idea that some behaviors are either largely genetically or environmentally determined (Alcock 1993). In animals such as birds, virtually all behaviors require both genetic information and environmental stimuli in order to develop. The difference between an innate and a learned behavior is not the amount of genetic or environmental determination, but the degree to which the behavior appears in its complete form the first time an animal reacts to a key stimulus (Alcock 1993). By this definition, specific aspects of a herring gull's prey-dropping behavior may be innate. Tinbergen (1960) suggested that the hardness of an item prompts the dropping response even in very young gulls that he observed dropping rocks. However, apparent innate behaviors such as elicitation of a dropping response by hard prey are often modified by experience. While a specific aspect of avian prey dropping may be either innate or learned, the complete behavior should have both innate and learned components according to the above definition. A behavior is learned if modifications to the behavior are traceable to specific experiences in the animal's life. In a complex foraging behavior such as prey dropping by herring gulls, age-related improvement of dropping efficiency would be an indication of a learned component since this would indicate that the behavior is being modified through experience. It should also be noted that foraging efficiency may increase with age due to maturational differences in skeleto-muscular development. However, since young gulls have relatively well-developed flying skills, it has been suggested that the disparity between adult and juvenile prey dropping ability in gulls is due to learning and experience rather than differences in physical maturation (Barash et al. 1975).

Previous studies examining prey dropping efficiency of gulls have suggested that there is a difference in height of drop depending on age and substrate used (Barash et al. 1975, Maron 1982). However, little is known about the mechanisms for such age-related changes. In particular, the specific components of dropping behavior that contribute to the observed improvement, and apparent increase of efficiency with age, are unknown.

Improvement in foraging skills with age is usually attributed to learning since individuals are changing or modifying their behavior based on environmental cues and prior experience (Marchetti and Price 1989, Wunderle 1991). The most widespread form of animal learning is trial-and-error learning in which the animal learns to associate its own behavior with feedback from the environment (Hinde 1970, Marchetti and Price 1989). Observational learning may also play a role in acquiring complex behaviors such as foraging location preferences and prey capture techniques (Marchetti and Price 1989). Whatever type of learning is involved in acquiring foraging proficiency, the time spent learning efficient behaviors is often costly. A time of low foraging efficiency necessary to develop more efficient cognitive and motor foraging skills can have profound effects on juveniles, usually in the form of higher mortality rates for young (Marchetti and Price 1989). It has been suggested that a period of low foraging efficiency, whether due to cognitive or morphological differences, acts as a selective force that removes the least efficient foragers before they reach breeding age (Ingolfsson and Estrella 1978, Jansen 1990, Annett and Pierotti 1999). Additionally, it has been suggested that lower foraging efficiency seen in young birds is the underlying mechanism for deferred breeding (Greig et al. 1983, MacLean 1986, Jansen 1990, Annett and Pierotti 1999) and that in at least three species of gulls, including herring gulls, adult foraging performance levels for a standard diet are not achieved until the spring of the bird's fourth year (MacLean 1986).

Objectives and background on prey-dropping herring gulls at Jamestown Island

My objective in studying age-related differences in prey-dropping behavior of herring gulls was to investigate the role of learning in this complex behavior. As stated above, there are many aspects of foraging behaviors that could account for the observed lower foraging efficiency of juveniles (Marchetti and Price 1989, Wunderle 1991). Herring gulls at Jamestown Island all forage at the same site on the same single species of sedentary organism. Thus, foraging site selection, prey species recognition and other prey characteristics were naturally held constant during my study. Prey selection, search methods and prey handling technique were potentially interesting aspects of this system in which to test for age-related improvement because: (1) Wedge clams occur in various sizes with larger clams containing more energy than smaller clams, making prey-size selection a potentially important variable; (2) Wedge clams have a patchy distribution throughout the mudflat making search methods important with respect to selection of a good foraging patch; (3) Since prey handling involves a complicated time and energy consuming technique (prey dropping), execution of this technique is particularly relevant.

Herring gulls dropping wedge clams at Jamestown Island are faced with several choices. When attempting to predict or compare choices that animals are making while foraging, using the framework of optimal foraging theory to set a biological yard-stick can be helpful. When faced with foraging decisions, animals often optimize certain important currencies, such as drop height, prey size or foraging patch selection, depending upon their needs (Cuthill and Houston 1997). This study was not an attempt to discover whether or not herring gulls forage on wedge clams optimally. However, since age-related foraging differences are the focus, using optimal foraging theory to compare foraging efficiencies of young and adult gulls can be useful. Optimal foraging theory predicts that animals will maximize energy gain and forage optimally. If young gulls show lower foraging efficiency than adults, this would suggest that they are foraging sub-optimally. Therefore, for all comparisons, the foraging of adult gulls will be considered the optimum. If young gulls are foraging sub-optimally this would be an indication that age-related improvement towards the theoretical optimum is occurring.

As stated above, one of the aspects of foraging efficiency I compared was prey selection. Wedge clams vary greatly in size and have correspondingly different levels of energy and breakability associated with these different sizes. Clams were classified by size class, which correlates directly with caloric content (D. Cristol, unpubl. data). Size was determined by the clam's length and width using the following linear regression formula derived from measurements on an initial set of 3000 clams:

$$\text{Size} = 0.541 + 0.002(\text{length} \times \text{width})$$

Size classes were categories that evenly divided the full range of clams ever found into an integer scale from 1 (smallest – approximately the size of a thumbnail) to 12 (largest – approximately the size of a tennis ball).

Wedge clams must be dropped onto a hard substrate in order to be consumed by the bird. This action requires energy, and if a gull fails to drop a clam from a sufficient height, another energy-consuming drop will be required to smash open the clam. Clams of different sizes vary in the amount of work necessary to crack them open by dropping, referred to as a clam's "breakability". Larger clams also yield more energy in the form of calories upon successful smashing, but are more awkward to transport. Based on the breakability, energy contained and difficulty in transporting different size classes of clams, gulls should probably be choosing a size 7 clam (D. Cristol, unpubl. data). This corresponds to the most disproportionately dropped size class of clam dropped at Jamestown Island (size 7), which was determined by comparing the size classes of wedge clams available in the mudflat and the size classes of those dropped on the road between 1996 and 1999 (D. Cristol, unpubl. data; see Appendix B). This prediction of which clam size class gulls should be choosing should not vary with the age of the gull since, in terms of caloric gain and difficulty in transporting larger clams, all ages of gulls should have nearly identical requirements and constraints as there is no body size variation with age in this species.

The question of the height from which prey should be dropped is confounded by several variables (Siegfried 1977). The optimal height of a given drop often depends on local factors including substrate hardness, kleptoparasitism pressure, prey breakability, height of previous drops (if any) and profitability of prey dropped (Cristol and Switzer 1999). Because of all of these factors, there may not be just one answer to the question of "what is the optimum height from which to drop a clam?" I held substrate hardness constant by including only those drops that occurred on the paved road at Jamestown Island. I also controlled for shell damage due to previous drops by only using the height of the initial drop when comparing drop heights. Kleptoparasitism pressure may be an important variable when determining how high an individual should take a clam on a single drop since height adjustments may lessen the chances of food being stolen. However, I was not attempting to predict a specific optimal height that gulls should be using for each individual drop. Rather, I was comparing mean drop heights of adult versus juvenile gulls as a measure of energy spent. Unless young and adults differed in the average amount of kleptoparasitism pressure they faced, the age-specific mean values of drop heights should not have been affected by random variation in kleptoparasitism pressure on particular drops. Thus, prey breakability and prey profitability were the two variables most likely to affect dropping performance of the gulls I studied. Since both of these variables vary with clam size class, I focused on recording the height of drop and the size of clam selected by age class of gull.

In summary, the overall objectives of this study were to answer the following questions: (1) Are there age-related differences in ability to select profitable-sized prey items? (2) Do juvenile herring gulls drop clams from a different height than adults? (3) If age-related differences in either size of clam dropped or height of drop occur in herring gulls, what are the mechanisms that explain this variation?

CHAPTER I

DIFFERENCES BETWEEN AGE CLASSES IN DROP HEIGHT AND PREY SIZE DROPPED

INTRODUCTION

Learning, morphological and neurological differences, and nutritional requirements can all play a role in age-related differences in foraging skill (Marchetti and Price 1989, Wunderle 1991). Herring gulls wintering at Jamestown Island, VA employ a foraging behavior known as prey dropping that has been described as cognitively complex (Beck 1980). This foraging behavior allows the bird to access food that is otherwise unavailable. Jamestown Island herring gulls drop wedge clams from the air in order to smash them open and access the meat inside. A gull must take a clam to a sufficient height to crack open the shell and must select a clam that has enough meat and calories so that a positive net energy gain is achieved. If a gull drops a clam from too low, additional drops and additional energy will be required to break open the clam. If a gull chooses a small clam of low caloric content, the energy gained from the clam may not offset the energy expended during the prey drop.

Differences between juvenile and adult foraging efficiency have been found in prior studies of prey-dropping gulls (Barash et al. 1975, Ingolfsson and Estrella 1978, Maron 1982). Furthermore, other prey-dropping avian species have been found to choose the most energetically profitable prey to drop (Zach 1979, Whiteley 1990). Based on these studies and previous observations of local herring gulls, I examined the age-related efficiency of herring gulls dropping clams with respect to drop height and prey choice. My objective was to answer the following questions: (1) Do juvenile herring gulls drop from different heights than adults? (2) Do juvenile gulls select different, less-profitable prey than adults? If drop height and prey size are important in terms of energy gained while foraging, then age-related changes in these variables would indicate that herring gulls are not born with an inherited set of rules for prey dropping; rather, they learn aspects of this complex foraging task. I predicted that juvenile gulls would drop clams from lower heights when compared to adult drop heights because lower drop heights are easier to achieve. Lower drop heights will result in fewer broken clams on the first attempt and thus ultimately require more energy in the form of additional drops. Furthermore, additional drops require more time handling the prey which increases the likelihood of theft or loss of the prey item. I also predicted that juvenile gulls would be less selective in the prey sizes they drop, choosing more of the abundant small clams.

The goal of this study was not to determine the optimal height from which herring gulls should drop wedge clams. Rather, it was to compare the performance of juvenile and adult herring gulls with respect to height of drop and size of clam. Improvement of prey-dropping efficiency with age would be an indication of learned components in this cognitively complex foraging behavior. Jamestown Island herring gulls are an ideal study subject for questions on learning and age-related improvement of foraging skills not only because this foraging behavior is so cognitively complex, but also because herring gulls go through four distinct basic plumages in their first four years of life (Appendix A), which allows for rapid and accurate aging of individuals in the field.

METHODS

I collected all data at Jamestown Island, James City County, Virginia from December 1998 through March 1999. The study site, located at the entrance to the National Historic Park's Jamestown Island Unit, is a tidal mudflat area that is submerged during high tide and exposed during typical low tides. The wedge clams that serve as the herring gull's prey are buried <3cm below the surface of the mud. The exact times at which I collected the data on a given day varied depending on the tidal cycle for that day. In general, all data collection occurred during daylight hours (between 0700 and 1800 hours) from two hours before low tide until one hour after, as this was the time span when the most mud was exposed each day. Herring gulls were only able to obtain live clams from the mud while it was exposed or had a very shallow layer of water over it. Herring gulls were almost never present at high or mid tides or when mud was not exposed due to easterly winds, excessive rains or unfavorable lunar cycles.

Foraging drops occurred either on the paved road that crosses the mudflat and provides access to the park, or on a small rocky island located on the southeast edge of the mudflat. The area of the mudflat that was usually exposed at low tide is roughly rectangular in shape and is approximately 270m x 120m. In order to drop clams on the paved road, gulls must fly from the mudflat across an area approximately 50m wide that is composed of a narrow band of marsh vegetation and an area of mowed lawn adjacent to the road. The road is at a higher elevation than the mudflat so the gulls must gain altitude in addition to that required for the drop if the road is used.

Each day data were collected, I recorded the weather conditions (temperature, wind speed and direction, cloud cover, precipitation) and the time of low tide. For each clam dropped by a gull, the age of the gull was recorded as either 1, 2, 3 or 4+ years (see Appendix A). I collected data on a gull only if it was dropping a clam that I had observed it obtaining from the mud. Data on drops of stolen or previously abandoned clams were not collected for this study. I only considered drops on the paved road in this study because (a) judging the height of a drop on an island that is 200m away is not very accurate and (b) I wanted to control for substrate hardness.

Controlling for substrate removed the possibility that the gulls adjusted drop height for hard or soft surfaces as shown in previous studies (Barash et al. 1975, Siegfried 1977, Cristol and Switzer 1999).

All heights were measured by one of two methods. Either: (1) the drop height was estimated by comparison to the known height of poles that had been erected along the side of the road where drops occurred. All poles were constructed of 3.81cm diameter PVC pipe and set into larger diameter PVC bases buried and cemented into the ground. Each pole rose exactly 4.57m above the level of the road and was marked with bright, fluorescent orange paint at 0.91m intervals. Six bases and poles were constructed along the east edge of the road approximately 30m apart and allowed for pole height estimations along approximately 200m of the road. (2) Alternatively, the drop was videotaped with a Canon ES6000, 8mm Video Camcorder and drop height was determined by replaying the video. I counted the number of video frames from when the clam left the gull's beak until it struck the ground. Each frame was a time interval of 1/30th of a second. This resulted in a very accurate measure of a clam's airtime in a given drop. From this time, I calculated the height of the drop to the nearest 0.15m using the following formula:

$$\text{Height} = V_0T + 0.5(GT^2)$$

Where V_0 is the initial velocity due to movement of the gull, T is time and G is the acceleration due to gravity (9.8 m/s^2). Based on filming drops from a known height on a building, it was previously determined that the small changes in initial velocity of the gull's head had no effect on calculated drop height using this technique for all drops $\leq$55 frames or 1.83 seconds of airtime (D. Cristol, pers. comm.). Since no drops greater than 55 frames were recorded in this study, I assumed $V_0 = 0$ and made no correction for initial downward velocity of the gull.

In addition to estimating the height of drops, I also collected dropped clams when possible to determine their size class. Dropped clams were collected only if I was able to reliably determine the bird's age and that it was dropping a clam that it had obtained directly from the mud. I then classified each clam into one of the 12 size classes by comparing it with a set of 24 cleaned exemplar clams. The clams in this exemplar set were selected to represent the entire range of sizes from 3000 clams dropped by gulls in 1996/1997, with each shell in the set representing the upper or lower limit for one of the 12 size classes (D. Cristol, pers. comm.). Any clam could then be classified by comparison to this exemplar set. In order to accurately classify a recovered, dropped clam using this exemplar set, one valve of the recovered clam was matched to the appropriately sized opposite valve in the exemplar set. The valve served as the primary match criterion when sizing a dropped clam using this method and the hinge of the dropped and recovered clam was used as a secondary match criterion. Both the valve and the hinge were fitted to the opposite valve of each member of the exemplar set until an accurate fit was found.

In many cases, birds would fly with a smashed clam to the mudflat and consume it there. This made it impossible to recover most dropped clams. Likewise, there were instances when filming or accurately estimating the height of a drop was impossible, but I was able to determine the gull's age and recover its dropped clam. Ideally, on a given drop, I recorded the age of gull, height of drop and size of clam but this was not always the case. All data points included age of gull and either size of clam, height of drop or both.

Data were analyzed in two ways. First I compared each of the four ages of gulls (1, 2, 3 and 4+), and then I lumped the older three age classes together as "experienced" and compared them to "naïve" yearling birds. I used a one-way analysis of variance on transformed data to test for significant differences between the four ages of gulls with respect to height of drop and clam size class dropped. To compare height of drop and clam size class dropped among experienced and naïve gulls, I used Welch's t-test, which does not assume that variances are equal between test groups. I then calculated the statistical power for all non-significant results to determine the likelihood of committing a Type II error. For each power analysis I calculated the likelihood of detecting a small difference between means and a medium difference between means as defined by the hypothesized effect sizes in behavioral comparisons for the statistical test in question (Cohen 1988). Power is presented after each non-significant finding, with the chance of detecting a small difference first followed by the chance of detecting a medium difference.

RESULTS

I recorded heights for a total of 93 drops. The heights of these drops, however, were not normally distributed (Shapiro-Wilk $W = 0.9402$, $p = 0.0005$). Therefore, these data were log-transformed by taking the natural log of the heights which resulted in a more normally distributed data set (Shapiro-Wilk $W = 0.9712$, $p = 0.19$). All data analyses were then performed on the transformed data.

There was no significant difference in height among all age groups (ANOVA, $f_{3,92} = 0.2172$, $p = 0.8842$, Table 2, Figure 1). Power for this non-significant result was 83% to detect a small difference and >99% to detect a medium difference, making the negative results of this ANOVA very reliable. Drop heights of older or experienced gulls also did not differ from that of yearling or naïve gulls (Welch's $t = 0.6643$, $df = 71.466$, $p = 0.5087$, Table 3, Figure 2). The power for this non-significant result was only 27% to detect a small difference, but was reasonable for detecting a medium difference between means (Power = 92%). In other words, there was only an 8% chance that a Type II error was committed if a medium difference between drop heights exists.

A total of 43 dropped clams of known size were recovered from gulls of known age. No significant differences were found when comparing mean clam size class dropped among the four ages of gulls (ANOVA, $f_{3,42} = 0.5391$, $p = 0.66$, Table

4). However, these results should be treated with caution since small sample sizes for all ages, particularly ages 2 and 3, resulted in low statistical power of 16% for detecting a small difference between means and 62% for detecting a medium difference between means. Clam size also did not differ significantly between naïve and experienced gulls (Welch's t = 0.9668, df = 39.464, p = 0.34, Table 5, Figure 3). This non-significant finding should also be treated with caution since the statistical power for this comparison is 15% to detect a small difference and 62% to detect a medium difference between means.

Although no significant differences in mean clam size classes dropped were found, naïve gulls did drop a broader size range of clams than experienced gulls. This is evidenced by the higher standard error of the mean and can be compared with sample sizes controlled by using the coefficient of variation (Table 5). The coefficient of variation for naïve gulls was 20.84 which differed significantly from the coefficient of variation for experienced gulls of 14.05 ($F_{23,18} = 3.023$, $p < 0.02$) (see Zar 1996: 144 for an explanation of this test). Yearling gulls dropped clams as small as size 3 and as large as size 9, while older gulls dropped only sizes 5 through 8.

TABLE 2

HEIGHT OF DROP FOR EACH AGE OF GULL

Age	n	Mean height (m) ± SE	Mean ln(height) ± SE
1	33	6.60 ± 0.43	1.82 ± 0.07
2	31	7.14 ± 0.47	1.90 ± 0.07
3	11	7.08 ± 0.96	1.87 ± 0.13
4+	18	6.98 ± 0.75	1.84 ± 0.11

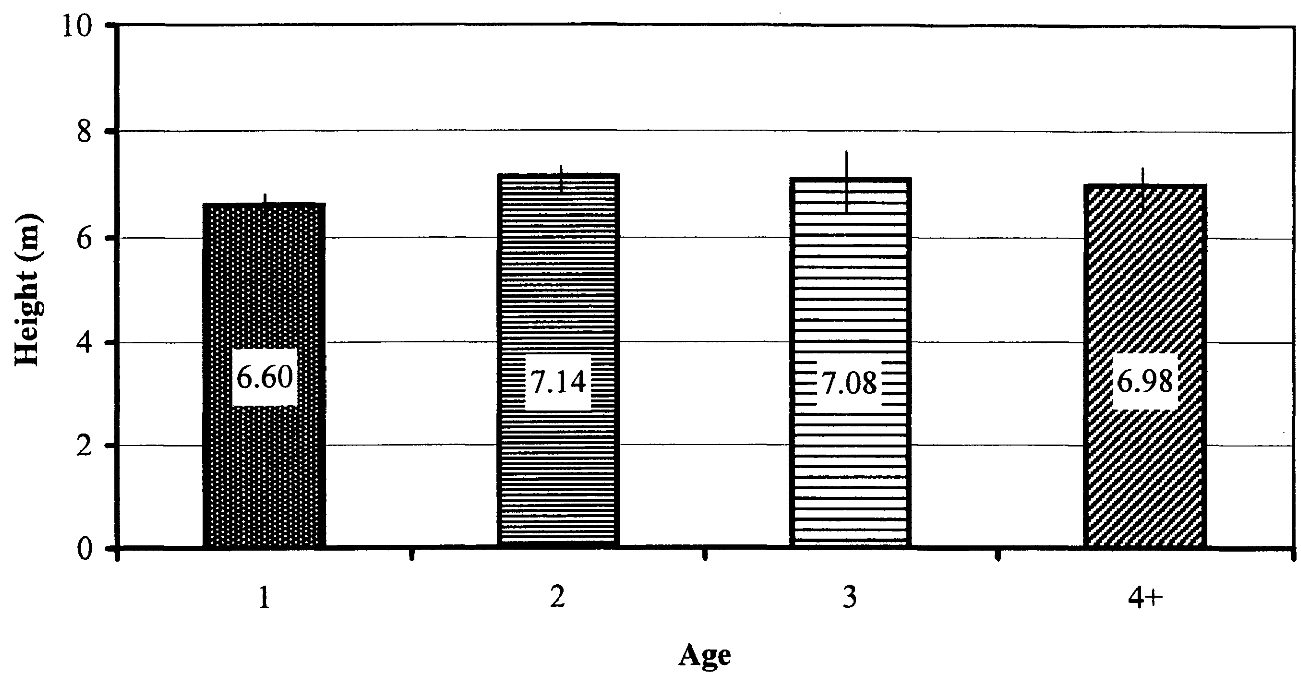
TABLE 3

HEIGHT OF DROP FOR NAÏVE AND EXPERIENCED (EXP) GULLS

Age Class	n	Mean height (m) ± SE	Mean ln(height) ± SE
Naïve	33	6.60 ± 0.43	1.82 ± 0.07
Exp.	60	7.08 ± 0.37	1.88 ± 0.05

FIGURE 1

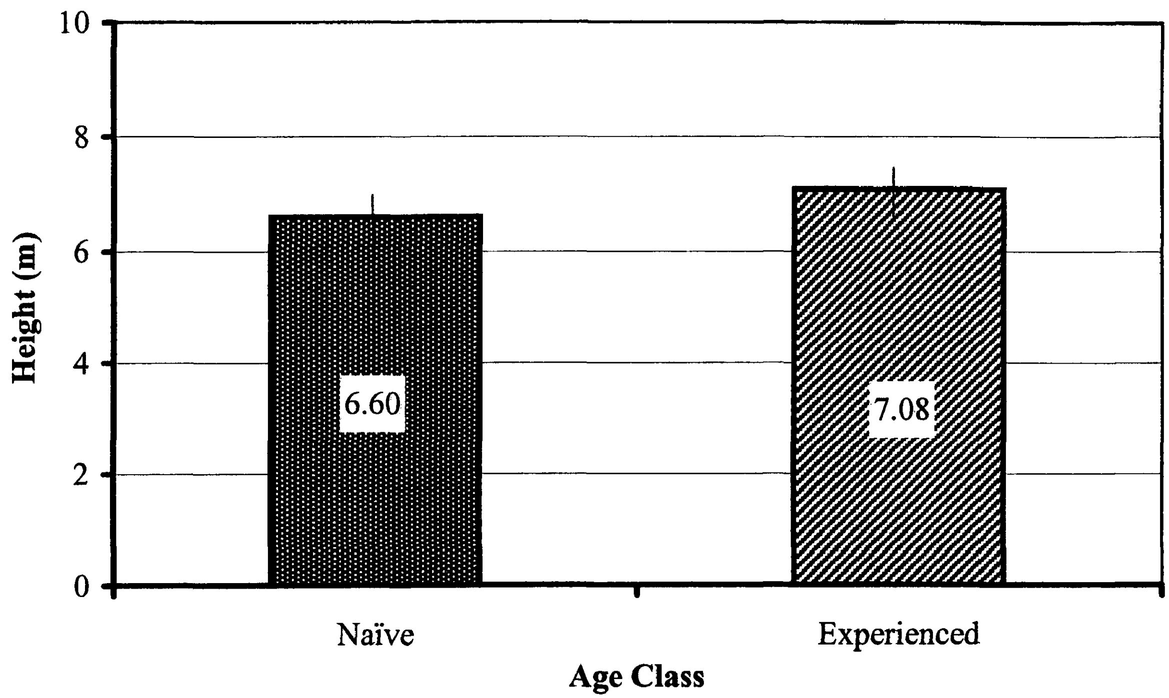
MEAN DROP HEIGHT BY AGE



Mean drop heights for all ages of gulls were not significantly different from each other (p=0.88). Statistical analyses were performed on the natural log of the drop heights rather than the actual heights that are presented above.

FIGURE 2

MEAN DROP HEIGHT BY AGE CLASS



Mean drop heights for yearling versus older gulls were not significantly different ($p=0.509$). Statistical analyses were performed on the natural log of all heights, not the actual heights shown above.

TABLE 4

CLAM SIZE CLASS DROPPED FOR EACH AGE OF GULL

Age	n	Mean clam size class ± SE
1	24	6.71 ± 0.29
2	6	6.17 ± 0.40
3	3	6.00 ± 0.58
4+	10	6.60 ± 0.27

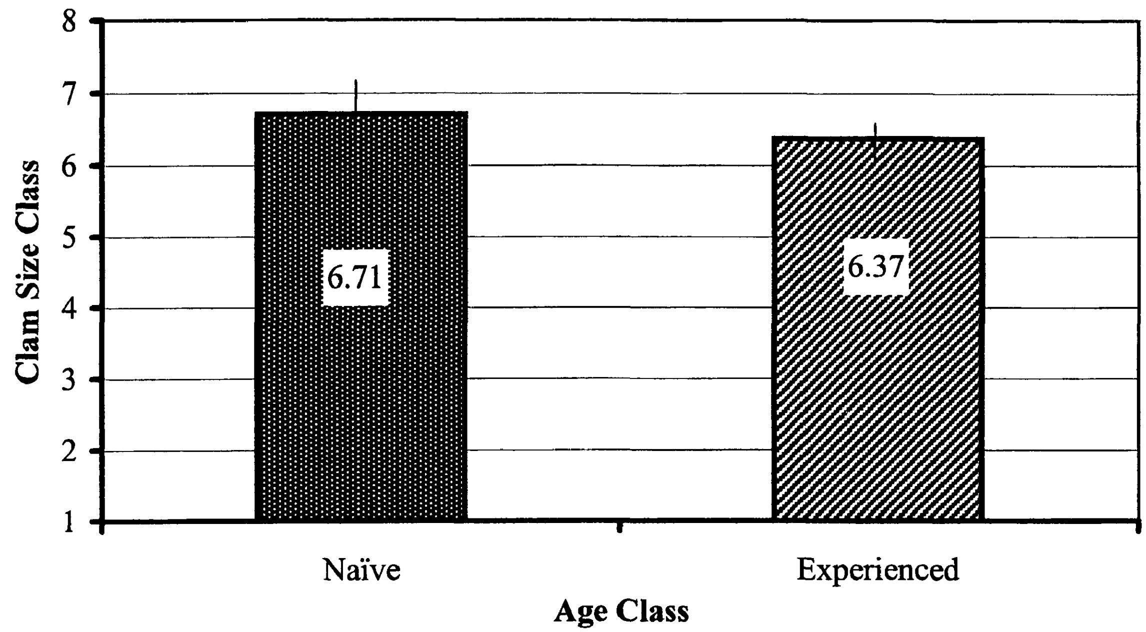
TABLE 5

CLAM SIZE CLASS DROPPED AND COEFFICIENT OF VARIATION FOR NAÏVE AND EXPERIENCED (EXP) GULLS

Age class	n	Mean clam size class ± SE	Coefficient of Variation
Naive	24	6.71 ± 0.29	20.84*
Exp.	19	6.37 ± 0.21	14.05*

FIGURE 3

MEAN CLAM SIZE CLASS DROPPED BY AGE CLASS



Means are taken from discrete integer size classifications for n=24 clams for yearling gulls and n=19 clams for older gulls. Means are not significantly different ($p=0.34$), but yearlings dropped a broader size range of clams (CV = 20.84 for yearlings, 14.06 for older gulls).

DISCUSSION

Young herring gulls dropped clams from heights that did not vary significantly from the heights of older, presumably more experienced gulls. Other studies have indicated that there is a tendency for yearling gulls to drop clams from lower heights than older gulls (Barash et al. 1975, Siegfried 1977, Maron 1982). Although the direction of the non-significant differences in my height data are consistent with these other studies, I can only conclude that young gulls are not far from exhibiting the same drop heights as experienced birds at this site. A larger data set might increase the statistical significance of the difference in drop heights, but for now there is little evidence that experience leads to changes in drop height.

There is also the possibility that first year herring gulls, being relatively new to flying, are less able to regulate the height to which they are taking clams for dropping due to inadequately developed flight skills. It would seem, however, that since juvenile gulls have well developed flight-ability, any disparity between their performance and that of adults when dropping prey is not caused by maturational factors. Rather, any disparities are likely the result of trial-and-error learning with juvenile gulls becoming better at choosing appropriate drop heights with age and experience. A larger data set is required to determine if the suggestion of a trend in my data are in fact indicative of real differences between ages, and if so, whether naïve birds are using lower heights as in other studies.

All ages of gulls dropped the same mean size class of clam (mean size class of all clams dropped by all ages = 6.56 ± 0.18). This is very close to the size indicated as the most disproportionately selected for dropping (6.8) based on approximately 6000 drops (pers. com. D. Cristol). However, yearling gulls dropped a much broader size range of clams than gulls ≥ 2 years of age. Clams as small as size 3 and as large as size 9 were recovered from first-year gull drops, whereas older gulls dropped clams from size 5 to size 8 only. This greater variation in clam size dropped by younger gulls suggests that they are less selective when choosing prey to drop than older gulls. First-year gulls may lack the prey assessment skills that older gulls have acquired through experience. However, they may be foraging in different parts of the mudflat with different size distributions of clams. The next two chapters address these questions concerning the disparity of size ranges of prey dropped by experienced versus naïve gulls.

In conclusion, there did not appear to be age-related differences in drop height for herring gulls dropping wedge clams at Jamestown Island. I have found no evidence of a learning component in terms of drop height for these gulls, but further studies with a larger data set might reveal trends in drop height that have been found in previous studies. Herring gulls of all ages appear to be dropping primarily clams of profitable size as is evidenced by observed means. However, yearling gulls are dropping a broader size range of clams which includes unprofitable clams. This suggests that younger gulls have poorer prey acquisition skills than adults due to either where they are foraging for prey or their ability to assess a prey's quality once it is obtained. The causes for these age-related differences in prey selection efficiency will be examined in the next two chapters.

CHAPTER II

DO PREY PATCHINESS AND SIZE DISTRIBUTION EXPLAIN OBSERVED DIFFERENCES IN PREY SIZE SELECTION FOR NAÏVE AND EXPERIENCED GULLS?

INTRODUCTION

First year birds chose a broader size range of clams than older birds (Chapter I). In this chapter I address the question of why first year gulls included more of the less profitable clams in their diets. What aspect of the prey selection process are first year birds lacking relative to the more efficient and experienced gulls? Are young gulls simply poor at choosing or are they encountering fewer preferred prey items due to differences in search methods or patch assessment skills?

The wedge clams that herring gulls drop at Jamestown Island could have an uneven distribution across the mudflat due to larval settlement patterns, patchy predation intensity or other factors. If clams are unevenly distributed with respect to size and overall density, then this patchiness, along with inexperience in a new foraging area may account for the broader size classes of clam being dropped by first year gulls. If yearling herring gulls are less able to determine where quality foraging patches are located, then they would be more likely to forage in a lower quality patch and encounter a greater number of less-profitable clams. This pattern of young birds foraging in lower quality patches has been seen in previous studies. Young herring gulls foraging at refuse sites were more dependent on older gulls for food location and showed a greater tendency to attempt kleptoparasitism while having less efficient foraging skills (Greig et al., 1983). This finding that naïve or young birds obtain information on the locations of good foraging areas is common in many other species such as pigeons (McLennan and MacMillan, 1986; Plowright and Redmond, 1996), red-winged blackbirds (Avery, 1994), snow buntings (Smith and Metcalfe, 1994) and gulls (Greig et al., 1983; Nuyts et al., 1996; Annett and Pierotti, 1999). Furthermore, searching and handling abilities in young herring gulls improve more slowly than other foraging abilities (MacLean, 1986). Because of the evidence for slower developing searching skills in herring gulls, I hypothesized that a patchy distribution of clams caused the difference in range of prey sizes dropped by naïve and experienced gulls. Yearling gulls with poor patch assessment and searching abilities will be more likely to forage in poorer quality patches and thus encounter more clams that are of less-profitable size.

To test this hypothesis, I determined whether clams were, in fact, unevenly distributed by size across the mudflat. If clam sizes are unevenly distributed, then juveniles should be foraging more often than adults in those areas containing fewer or less profitable clams. Any difference in distribution of foraging yearling and older gulls due to such a patchy distribution of clams with respect to size could be due to two possible factors. First, naïve gulls could simply lack the experience of searching for clams in the mudflat and thus lack the knowledge of where the best clams are located. If this is true, then naïve birds should forage in a more random pattern than experienced gulls, while the latter should concentrate their search efforts in the more profitable areas. Alternatively, there may be a dominance hierarchy in which older, more experienced gulls exclude naïve, yearling gulls from the more profitable areas. In this case, yearling gulls should be foraging in poorer quality areas of the mudflat and attempts to forage in areas with more profitable clams should result in agonistic encounters between gulls. In a dominance hierarchy such as this, experienced gulls should win any encounters that occur. Dominant gulls would then retain their control of better foraging patches.

METHODS

With the assistance of Michael Curatola, I collected data on clam densities and size distributions in October, 1999. I also censused gulls occupying the mudflat area from November, 1999 through March, 2000. Censuses were conducted during specified times at Jamestown Island (see methods section in Chapter I for a description of this site).

Before censusing for either gulls or clams, the mudflat area where gulls search for wedge clams was divided into 35 quadrats with dimensions of 30m x 30m for each quadrat. This resulted in a large rectangular grid with an area of 270m x 120m divided into four rows and nine columns (see Figure 4). The corners of each quadrat were marked by 1.5m galvanized conduit pipes that were buried approximately 1m in the mud. Due to the irregular shape of the shoreline, the quadrat designated as 9A was not included as it was not in the mudflat.

Clams were surveyed during September and October, 1999, before gulls returned from their breeding areas. Clam surveys were conducted primarily as a three-person effort with two individuals digging for and measuring clams and a third recording sizes of clams, number of clams found and the area required to find at least 15 clams. We searched for clams by randomly placing a sampling rectangle of 1m x 0.5m down in the quadrat of interest. Generally there were two searchers performing this task at once. Searching was done by digging with bare hands through the entire area of mud covered by the sampling rectangle until all clams contained within the sampling area had been located. This search continued in each quadrat until at least 15 clams had been found. The length and width of the first 15 clams were then measured and the clams were classified by size (see General Introduction for discussion of clam size classes). Once 15 clams were found, the last sampling rectangle was searched until no more clams were found and the total number of $0.5m^2$ samples as well as the total number of clams in those samples was recorded. Overall density was calculated from the total number of clams recovered per square meter.

Once clam densities and sizes were determined, a quadrat quality score (QQS) was assigned to each quadrat (Figure 4). The QQS is based on the mean preference score of the size classes of the first 15 clams found in the quadrat and the overall density of clams in the quadrat. QQS was calculated by assigning each of the first 15 clams in a given quadrat a preference score based on its size class (see appendix B), and then calculating the mean clam size class preference score for that quadrat from the 15 preference scores. This mean preference score for the quadrat was then multiplied by the density of clams in the quadrat (clams/m^2). Thus, QQS is highest with densely distributed clams of the sizes most disproportionately chosen by gulls and lowest with more dispersed clams of sizes not often selected by gulls.

Gull censuses were conducted from November, 1999 and March, 2000 approximately one hour before low tide. A spotting scope was set up at designated spots along the main road going out to the island for each gull census. These designated spots were marked with a tent stake that was boldly marked with flagging tape and were placed approximately in line with columns 2, 5 and 8 (refer to Figure 4). All herring gulls present in each quadrat were aged and classified as foraging or non-foraging depending on whether they were actively searching for clams. Furthermore, all gull species present in each quadrat were recorded in each census as

FIGURE 4

SCHEMATIC DIAGRAM OF THE MUDFLAT PLOT BY QUADRATS

D	2.578	3.480	1.362	3.712	1.405	5.355	2.669	0.984	3.500
C	5.076	1.296	2.003	1.266	3.040	1.314	0.853	1.725	0.016
B	0.548	1.054	-0.204	0.173	1.415	0.072	0.219	0.927	-0.153
A		0.784	0.418	0.154	0.530	-1.818	-1.152	0.524	-0.667
	9	8	7	6	5	4	3	2	1

The above numbers are quadrat quality scores (QQS) for each quadrat. A higher score indicates a higher quality quadrat. Quadrats were approximately 30m x 30m or 900m^2. Quadrat 9A was not included since it was not in the mudflat due to the shape of the shoreline.

well as weather conditions (air temperature, wind direction and speed, precipitation, cloud cover, time of low tide) and the pattern of water covering the mudflat area (if any).

The raw QQSs did not significantly differ from a normal distribution (Shipiro-Wilks W = 0.9429, p = 0.09) so these numbers were used in all data analyses. All gulls counted in the mudflat were assigned the QQS value corresponding to the quadrat in which they were present. Data was analyzed in two ways. First, the mean QQS of all naïve (age = 1) gulls, and that of all experienced (age $\geq$ 2) gulls were compared using Welch's t-test. Then the mean QQS of only the foraging naïve and experienced gulls were compared to each other also using Welch's t-test. Non-foragers were included in the data analysis because, although we observed no attempt by the gull to locate clams during the census, their location may have been indicative of where they normally forage for clams or where they had been searching for clams just moments before being counted. Power analysis was performed on all findings that were non-significant (see Chapter I for an explanation of power analysis).

RESULTS AND DISCUSSION

Clams were distributed unevenly throughout the mudflat area with quadrat quality scores (QQS) ranging from –1.82 to 5.36 with a mean QQS of 1.27 $\pm$ 0.27.

Higher quality quadrats in general were located along the western edge of the mudflat furthest away from the shoreline (Figure 4). A higher QQS indicates that the quadrat was of higher quality in terms of clam density and clam sizes.

I counted a total of 181 older gulls, which had a mean QQS of 2.30 ± 0.09 and 64 yearling gulls with mean QQS of 2.43 ± 0.18 (Table 6). There was no significant difference between the QQS of naïve and experienced gulls for all gulls censused (Welch's $t = 0.6616$, $df = 98.8$, $p = 0.51$, Figure 5). Sample sizes were smaller for analysis of foraging gulls only, with 76 older gulls, which had a mean QQS of 2.40 ± 0.15 and 38 yearling gulls with mean QQS of 2.38 ± 0.24 (Table 6). Again, there was no significant difference between QQSs for naïve and experienced gulls (Welch's $t = 0.0496$, $df = 66.28$, $p = 0.96$, Figure 5). Power analysis of feeding gulls indicated that results are reliable with the current data set, as there is a 71% chance of detecting a small difference between means and >99% chance of detecting a medium difference.

Since the mean QQS for all gulls (2.33) and foraging gulls only (2.39) were both higher than that of the average patch (1.27), I can conclude that gulls concentrated their foraging efforts in the better quality patches ($t = 12.94$, $df = 244$, $p < 0.0001$ for all gulls; $t = 8.78$, $df = 113$, $p < 0.0001$ for foraging gulls only). There were no observed dominance interactions, lending no support to the hypothesis that dominant adults were excluding subordinate young from the quality foraging patches. Higher densities of foraging gulls might result in competition for quality foraging patches or food resources in general as seen in previous studies (Monaghan 1980,

FIGURE 5

NUMBER OF NAÏVE AND EXPERIENCED (EXP) GULLS COUNTED PER QUADRAT WITH CORRESPONDING QUADRAT QUALITY SCORES

D	2.578 Exp = 3	3.480 Naïve = 3 Exp = 5	1.362 Naïve = 1 Exp = 5	3.712 Naïve = 1 Exp = 3	1.405 Naïve = 3 Exp = 17	5.355 Naïve = 4 Exp = 7	2.669 Naïve = 7 Exp = 30	0.984 Naïve = 11 Exp = 51	3.500 Naïve = 21 Exp = 48
C	5.076	1.296 Naïve = 1 Exp = 1	2.003 Naïve = 1	1.266 Naïve = 1 Exp = 3	3.040	1.314 Naïve = 3 Exp = 3	0.853 Exp = 1	1.725	0.016 Naïve = 2
B	0.548 Naïve = 1	1.054	-0.204	0.173	1.415 Naïve = 1	0.072 Exp. = 1	0.219 Naïve = 1	0.927 Naïve = 1 Exp. = 1	-0.153 Naïve = 1
A		0.784	0.418	0.154	0.530	-1.818	-1.152	0.524	-0.667
	9	8	7	6	5	4	3	2	1

Above numbers are for all birds counted without regard to foraging activity. The top number in each quadrat is the QQS for that quadrat. Quadrats where no gulls were ever counted are shaded in light gray. Note that birds were never observed in some very high quality quadrats (9C and 5C). Foraging was concentrated primarily in row D and columns 1,2 and 3.

Burger and Gochfield 1981, Greig et al. 1983). For now there is no evidence that older gulls are excluding yearlings from profitable foraging areas in the mudflat. In fact, if I had observed agonistic encounters over foraging patches, it is not clear from other studies whether it would be the young or the adult gulls that would dominate. In general, adult male herring gulls are believed to be dominant to females and juveniles in terms of food resources (Monaghan 1980) and are both more successful at and less susceptible to intraspecific kleptoparasitism (Burger and Gochfield 1981). However, there is conflicting evidence in terms of which gulls dominate foraging patches since, in at least one case, it is the young gulls that appear to control higher quality areas, displacing adults into secondary foraging patches (Steele and Hockey 1995). This may be due to a different dominance hierarchy or due to differences in foraging patch quality between these studies. Regardless of which age class would be dominant on the mudflats at Jamestown Island, it appears that herring gull densities were not high enough to make intraspecific competition for foraging patches a factor in patch use and thus, such competition cannot explain the difference in prey size ranges dropped by yearling versus older gulls.

Although some gulls were observed in patches of lower quality, and the birds in lower quality patches were primarily yearlings (Figure 5), mean QQS scores showed no indication of a difference in overall foraging patch selection by age class. Therefore, patchy distribution does not seem to account for observed differences in prey size selection between yearling and older gulls. While this does not answer the question of whether or not yearling gulls are able to assess the quality of a patch on their own, it does indicate that, on average, yearling gulls are not foraging in less profitable patches. Yearling gulls may be choosing foraging areas based on where older, more experienced gulls are searching for clams. However, regardless of why they forage in these areas, there is no difference in foraging patch quality between the two age classes. Further investigations to determine the cause of young gulls choosing less profitable prey will examine yearling gulls' ability to assess individual prey as profitable or unprofitable when presented with a choice of two different sized clams (see Chapter III).

Finally, it should be noted that after sampling the mudflat area for clams in each quadrat, the average area searched per quadrat was approximately 3m^2 and ranged from 2m^2 to 11m^2 with a standard deviation of 2.4. While this means that a very small percentage of each quadrat was sampled (an average of 0.39% sampled in each quadrat), I feel that my sampling regime was appropriate. Indeed, gulls concentrated their foraging efforts in the northwest corner of the mudflat, which was an area revealed as being of high quality by my sampling regime (Figure 5). Furthermore, examining the QQS across the mudflat indicates that changes in quality occur over a large scale with quality increasing further from shore in general.

TABLE 6

QUADRAT QUALITY SCORES FOR BOTH AGE CLASSES OF ALL GULLS PRESENT AND FORAGING GULLS ONLY

	Foragers and Non-foragers		**Foragers Only**	
Age Class	**n**	**Mean QQS ± SE**	**n**	**Mean QQS ± SE**
Naïve	64	2.43 ± 0.18	38	2.38 ± 0.24
Exp.	181	2.30 ± 0.09	76	2.40 ± 0.15
All Ages	245	2.33 ± 0.08	114	2.39 ± 0.13

CHAPTER III

AGE-RELATED DIFFERENCES IN PREY SIZE PREFERENCE

INTRODUCTION

Yearling and older gulls differ in the size range of clams that they drop. This difference does not appear to be due to either a difference in ability to locate high quality patches of clams in the mudflat or exclusion of young birds by older gulls from high quality patches (see Chapter II). In this study I tested the hypothesis that yearling gulls, when faced with a choice between better or worse prey items, cannot distinguish the profitability of the prey as well as older gulls.

Experience in foraging can affect many skills including the quality of individual prey items selected by an individual forager (Verbeek 1977, Greig et al. 1983, Richardson and Verbeek 1987, Amat and Aguilera 1990). Birds employing prey-dropping behavior are faced with several decisions including which prey to drop. If they choose a prey item that is too small, it may not contain enough energy to offset the energy spent finding and smashing open the prey item. If they choose a prey item that is too large, there may be handling problems and they may have to expend more energy in breaking the prey open. Many avian species employing prey-dropping behavior do forage optimally with respect to prey size dropped by choosing the most energetically favorable prey (Siegfried 1977, Zach 1978, Kent 1981, Whiteley et al. 1990). Although the mean clam size class dropped in this study did not differ significantly among age classes, there is a significant difference between the coefficients of variation in the size classes of clams dropped by naïve and experienced herring gulls. This suggests that naïve gulls are less selective than experienced gulls and drop less profitable clams more often. Identical means may be a result of where the gulls forage since all ages of gulls tend to concentrate their search efforts in the patches with higher densities of profitable clams (see Chapter II).

All clam size classes have a corresponding preference score (see Appendix B). The preference score is an indication of the proportion of clam size classes dropped by all gulls with respect to the proportion at which the clam size class occurs in nature. It should be noted that this is a preference score assigned to each size class without respect to age of gulls dropping the clam. Size classes with high preference scores indicate a clam size class that is disproportionately dropped at Jamestown Island, VA with respect to its abundance there. Clams of size class 7 and 8 are dropped at disproportionately greater frequency than other size classes and are also thought to be the most profitable size class of clam in terms of breakability, calories and ease of transport (D. Cristol, unpubl.data). I expected first year gulls to select clams randomly when presented with a choice between a clam of size class 7 or 8 and a clam with a lower preference score. Conversely, if prey selection improves with experience, older gulls (gulls $\geq$ 2 years) should select size class 7 and 8 clams significantly more often than expected by chance.

METHODS

I attempted to present clams in pairs to the gulls wintering at Jamestown Island from December 1999 through February 2000. I constructed a pair of small floating presentation platforms made of plywood, weather-treated lumber, pressed Styrofoam and duct-tape. Each platform was approximately 0.61m x 0.61m and had two pontoons attached to the bottom. This allowed the platform to glide over mud and provided buoyancy to float and glide on top of water as well. The platforms were operated from the shore or from a stationary platform in the mudflat and were moved by human power by way of a rope and pulley system. This system allowed for one platform, having a pair of clams on it, to be placed out into the mudflat while the second was being retrieved after a gull had made a clam selection.

Pairs of clams were kept separated on the deck of each platform byway of a wooden frame that gave each clam its own compartment and limited the amount they would roll. Although the presentation apparatus was effective in putting clams out into the mudflat in pairs, the birds showed little interest and in many cases aversion to the presentation apparatus. Gulls avoided the presentation platforms despite repeated use of fish heads and bread to attract the birds. Human presence in the mudflat area, which is required to operate the presentation apparatus also resulted in cessation of foraging activity and often gulls would simply abandon the site altogether.

After the unsuccessful attempts to present Jamestown Island herring gulls with pairs of clams, I decided to conduct clam choice experiments on a population of herring gulls that is more accustomed to close human activity. I presented pairs of clams to herring gulls in a mixed-age flock at a boat launch in Poquoson, VA. In each clam pair, there was always a clam that was of a disproportionately dropped size class, which was either a size 7 or size 8 clam. The other clam was either a small clam of size 5 or 6, or it was a large clam ≥ 9. I presented the clams to the gulls using a 60cm length of two-by-four lumber marked boldly on either side with an "S" and a "B". The smaller clam in the pair was always placed on the "S" while the bigger clam was placed on the "B". I placed each clam pair exactly 45cm apart on the board for each presentation. I also alternated the left-right orientation of the presentation board on successive trials to avoid bias.

A choice was recorded upon the first gull approaching the board and attempting to pick up one of the clams regardless of whether or not the gull flew off with the clam and dropped it. Physical contact with beak in an attempt to grab the clam was the criterion for a choice. Once a clam was moved, I recorded no further choices until the pair was reset or a new pair was laid out. Upon each choice, the following data were recorded: (1) the age of the gull choosing; (2) the number of gulls within 3.05m of the chooser; (3) the distance to the nearest gull; (4) the total number of gulls in the area. The number of gulls in the area and the approximate distance to nearby conspecifics was used to calculate a quantitative theft pressure index with which to compare how rushed or deliberate a choice might have been. In addition, I rated each choice subjectively as either "rushed" or "deliberate". A deliberate choice was assigned when the gull was able to inspect both clams and picked one without harassment from other gulls or was able to establish dominance before the choice was made. Rushed choices were those in which harassment occurred while the choice was made, a clam was taken while the gull was still in flight or the selection took ≤ 2 seconds. The subjective score of rushed or deliberate is an important distinction because even though the number of gulls present and their proximity to the chooser gives an indication of how rushed a choice might have been through a theft pressure index, it does not take all factors into account. Some gulls were able to establish dominance at the presentation board. These gulls made choices that appeared very deliberate despite subordinate gulls being in very close proximity (<1.5m away).

Since the difference in ranges of prey sizes dropped was seen between yearling gulls versus those ≥ 2 years of age, all data was analyzed as yearling versus older gulls. I used a binomial sign test, setting $p = 0.5$ for the null hypothesis to test if either yearling or older gulls were choosing clam sizes that were disproportionately dropped over either smaller and larger clams.

RESULTS

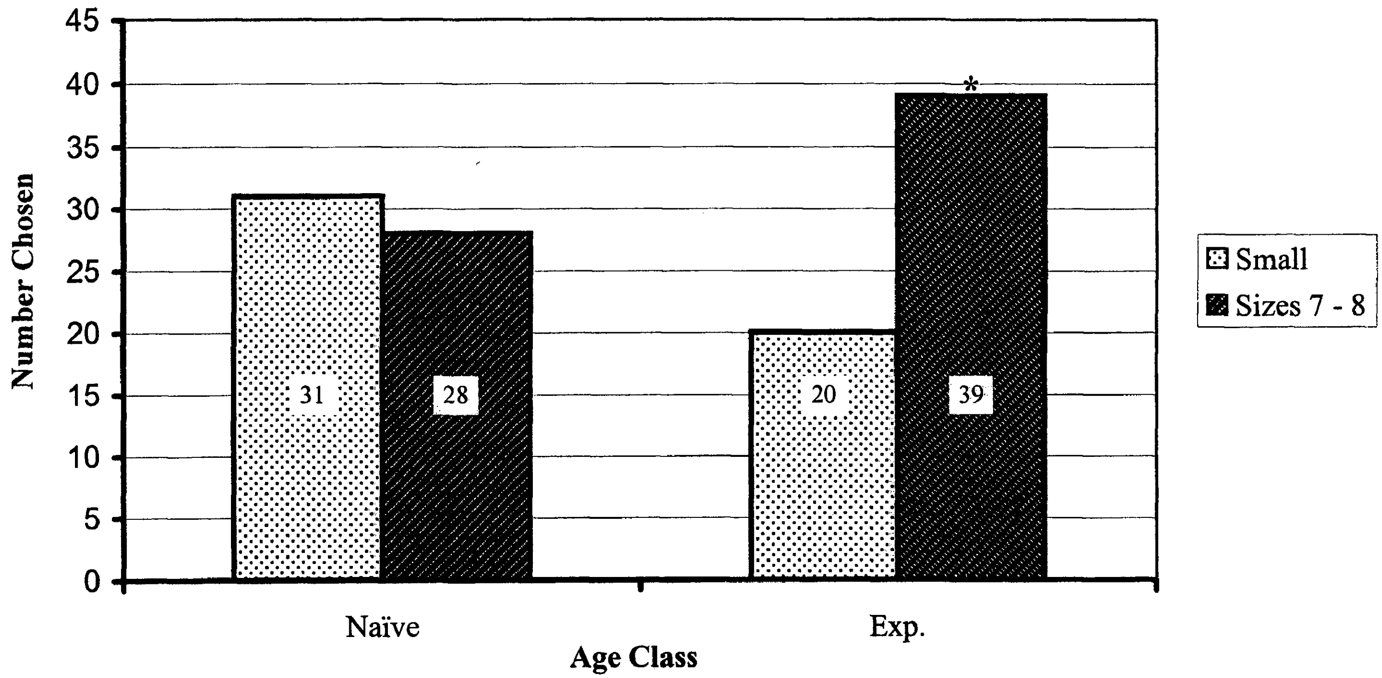
I tested for correlations between the subjective score of rushed or deliberate and the quantitative data collected on number of gulls in the area, number of gulls within 3.05m of the chooser and distance to nearest gull. I used logistic-regression analysis to determine if there were any significant relationships between theft pressure and a gull's tendency to make a deliberate or a rushed choice. I found no significant relationship between total number of gulls in the boat launch area and a gull's apparent rushed or deliberate choice (Chi Square = 1.046, $p = 0.31$). However, both distance to nearest gull (Chi Square = 16.276, $p < 0.0001$) and number of gulls within 3.05m of the chooser (Chi Square = 6.425, $p = 0.011$) were significantly correlated with the subjective score. When a conspecific was $\leq$0.61m from the chooser, a rushed choice was more likely to result. Furthermore, when there were $\geq$4 gulls within 3.05m of the chooser, a rushed choice was more likely to result. Because of these correlations, I analyzed data in two ways. First, I used all choice data collected regardless of whether or not the choices were assessed as deliberate or rushed. Then, I analyzed the data using only deliberate choices. This ensured that the results would be indicative of an actual choice rather than a rushed reaction. Examining all choice data whether the choices were rushed or deliberate is still useful for two reasons. First, it increases sample sizes giving more strength to findings if they do not contradict the deliberate choice data. Furthermore, an apparent rushed choice due to the proximity of conspecifics does not guarantee that accurate prey assessment was prevented.

I collected data on a total of 177 choices for all age classes of gulls. In 59 trials of naïve gulls choosing between disproportionately dropped (size 7 - 8) and small (size 5 - 6) sized clams, there was no significant difference between the two size groups with 31 small clams being chosen versus 28 size 7 – 8 clams (binomial sign test, p=0.79, Figure 6). Power analysis for this non-significant result indicates that with the current sample size, there is a 17% chance for detecting a small difference and a 74% chance for detecting a medium difference. Examining these data using only deliberate choices also shows that naïve gulls had no preference for size 7 – 8 clams (binomial sign test, p = 0.88), as they choose small clams in 23 of 46 trials. Power analysis for this non-significant result indicates that with current sample sizes there is an 11% chance of detecting a small difference and a 63% chance of detecting a medium difference, but there was no hint of a difference.

Data on 59 choices of experienced gulls ($\geq$ 2 years) choosing between small and disproportionately dropped clams showed a significant preference for the size 7 - 8 clams (binomial sign test, p = 0.019, Figure 6), with 20 small clams chosen versus 39 size 7 – 8 clams. Using only deliberate choices yields similar results (binomial sign test, p = 0.020), with experienced gulls choosing small clams a total of 15 times and size 7 - 8 clams a total of 32 times out of 47 trials.

FIGURE 6

NUMBER OF SMALL VERSUS DISPROPORTIONATELY DROPPED CLAM SIZES CHOSEN



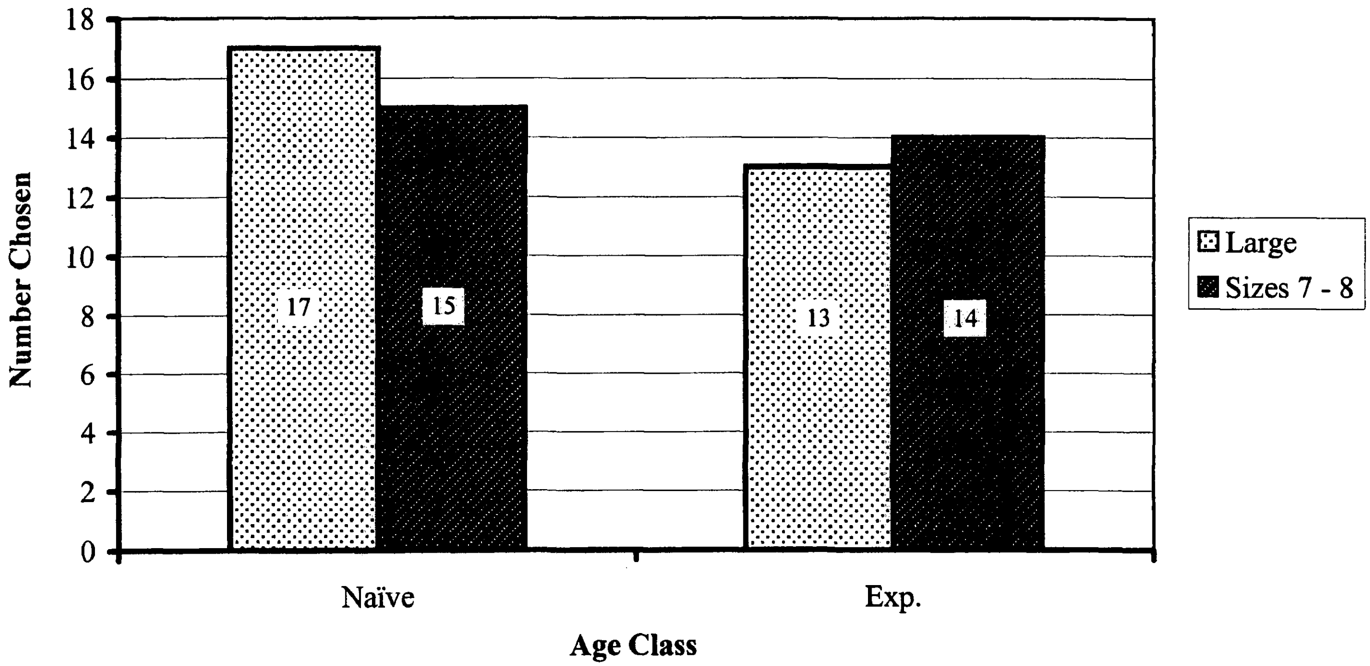
Above numbers are for all choices observed. Only the choices of the experienced gulls deviated significantly from what would be predicted by chance. Analysis of deliberate choices only gives similar results with smaller sample sizes.

Naïve gulls choosing between large ($\geq$9) and disproportionately dropped (size 7 - 8) clams showed no preference (binomial sign test, p = 0.86, Figure 7) in 32 trials, having chosen 17 large clams and 15 size 7 or 8 clams. These non-significant results should be treated with some caution since power analysis indicates that there is only a 15% chance of detecting a small difference and a 55% chance of detecting a medium difference with the current sample size. Examining only the deliberate choices also gives non-significant results (binomial sign test, p = 0.67) with 10 large clams chosen in 23 trials. Again, this non-significant result should be treated with caution as power analysis indicates only a 9% chance of detecting a small difference and a 40% chance of detecting a medium difference with current the sample size.

Experienced gulls also showed no significant preference between large sized clams and disproportionately dropped clams (binomial sign test, p > 0.99, Figure 7) with 13 large clams and 14 size 7 - 8 clams chosen out of 27 trials. Power analysis on this non-significant result indicates that there is a 15% chance of detecting a small difference and a 52% chance of detecting a medium difference. Again, an analysis of deliberate choices only yielded similar non-significant results (binomial sign test, p = 0.84) with 11 large clams and 13 size 7 or 8 clams chosen out of 24 trials. Statisitical power was again low due to a small sample size with an 8% chance of detecting a small difference and a 36% chance of detecting a medium difference.

FIGURE 7

NUMBER OF LARGE VERSUS DISPROPORTIONATELY DROPPED CLAM SIZES CHOSEN



Above numbers are for all choices observed. Neither experienced nor naïve gulls deviated significantly from random chance when choosing between large or size 7 - 8 clams. Analysis of deliberate choices only gives similar results with smaller sample sizes.

DISCUSSION

Based on the data collected on prey selection when presented with a choice, it appears that naïve herring gulls lack the individual prey assessment ability of older, more experienced conspecifics. Yearling gulls did not significantly deviate from the predicted random proportions, indicating no preference in clam size. Thus, naïve gulls appear to choose clams indiscriminately with regards to their profitability. Experienced gulls, however, did not select clams randomly for all choice tests. There was a significant deviation from the null hypothesis of equal proportions of clams chosen when experienced gulls were presented with small (sizes 5 and 6) and disproportionately dropped (sizes 7 and 8) clams. As predicted by the alternate hypothesis, experienced gulls chose the more profitable size 7 - 8 clams significantly more often than smaller clams. This suggests that older gulls are able to distinguish between a clam that will yield a greater amount of calories and a clam that may prove to be an energetically poor choice in terms of net energy gain.

All gulls appeared to choose large (size 9+) and disproportionately dropped (sizes 7 and 8) clams with equal frequency. This suggests, in light of the findings for small versus size 7 – 8 above, that young gulls are still choosing indiscriminately and not assessing the prey or its quality before choosing. However, it is particularly interesting that older gulls appear to make random choices when presented with large and size 7 - 8 clams since they selected size 7 - 8 clams over smaller clams. This seems to indicate that experienced gulls have developed a selection criterion where if a clam is of a certain size or greater, it is acceptable prey to drop. However, if the clam is below this critical size, the prey is not worth the energy expended to smash it open because the risk of net energy loss is too great.

The evidence for a lack of accurate prey assessment ability in naïve gulls presented here could explain why yearling herring gulls at Jamestown Island drop a broader size range of clams than older gulls. However, it is interesting to note that, while yearling gulls did drop clams of low profitability, the mean size class dropped by first year gulls was not significantly different than that of gulls ≥ 2 years or that of the predicted preferred size of 7. This could be due to the patchy distribution of clams in the mudflat since all ages of gulls foraged primarily in similar, high-quality patches. It seems unlikely, however, that naïve or inexperienced gulls would be able to assess overall patch quality and concentrate in these quality patches with no prior knowledge of the foraging grounds. Yearling gulls foraging on clams at Jamestown Island may be relying on the foraging behavior of experienced gulls when selecting foraging patches. In fact, young herring gulls foraging at refuse dumps select profitable foraging patches based on where older conspecifics are foraging but are still less successful in choosing more profitable food items in these quality patches (Greig et al. 1983). These findings agree with mine and it is unlikely that yearling herring gulls could take cues such as what size clam to drop simply by watching older conspecifics. Such fine assessment of prey quality is likely gained from trial-and-error learning, which would account for the differences in prey dropped by first year versus older herring gulls. Therefore, it appears that the difference in prey size ranges dropped by first year versus older gulls is due to inexperience and lack of developed prey assessment abilities in first year gulls. Only through repeated drops, including drops of clams that do not yield a positive net energy gain, would gulls develop accurate prey assessment abilities through trial-and-error learning.

GENERAL DISCUSSION

Herring gulls of all age classes drop clams at Jamestown Island. I examined age-related differences in this foraging behavior with respect to height of drop and size of clam dropped. Previous studies on prey-dropping behavior have shown that drop height and prey size can affect net energy gain from foraging drops (Siegfried 1977, Zach 1978, Zach 1979, Maron 1982, Richardson and Verbeek 1986, Whiteley 1990, Ward 1991, Cristol and Switzer 1999). Since young birds in general tend to forage less efficiently than adults, I chose these important currencies in order to determine if age-related differences in prey dropping efficiency exist in herring gulls and how any such differences might be explained.

I found no significant differences in drop height among the four ages of herring gulls. There was similarly no difference in height of drop between naïve (age = 1) and experienced (age ≥ 2) gulls. Although past studies of prey dropping species have shown a difference in drop height with age (Barash et al. 1975, Siegfried 1977, Maron 1982), I found no such differences. This may have to do with the physical aspects of the prey being dropped by these gulls and the substrate onto which the prey is being dropped. Jamestown Island herring gulls drop wedge clams onto a paved road to smash them open. In most cases, the clams crack or shatter on the first drop.

Because wedge clams are so brittle and likely to break on such a hard surface, drop height may not be an important variable in terms of maximizing energy gain from foraging drops as it is in other systems (Barash et al. 1975, Siegfried 1977, Zach 1979, Maron 1982, Whiteley 1990, Cristol and Switzer 1999). These previous studies that have found that drop height is an important variable have all been on systems that usually required repeated drops of the prey items before they broke open.

Mean clam sizes also did not significantly differ between age classes of gulls or between yearling and older gulls. However, yearling gulls did tend to drop a broader size range of clams, which included clams of low profitability. Older, and presumably more experienced, gulls showed less variation in the sizes of clams they dropped. This difference in prey size selection appears to be due to a lack of adequate prey assessment skill in naïve gulls. When presented with a choice between small and more profitable clams, yearling gulls selected clams randomly while older gulls selected the larger, more profitable prey more often than would be expected by chance. It appears, from the data, that older gulls have developed a selection criterion for choosing prey to be dropped. If the prey is of a certain size, approximately size 7 - 8, it appears to be more valuable than a smaller clam with respect to the inherent risks and energy expenditures incurred when dropping the clam. Anything larger than this critical size also appears to be acceptable since older gulls did not show a preference for size 7 and 8 clams versus larger clams. However, the results indicating a failure to discriminate against clams that may be "too large" should be treated with caution as the power for detecting small and medium differences was low for the analysis. Furthermore, the non-significant result may have been an artifact due to the preference tests having been performed in a parking lot where clams did not have to be transported over long distances. The cost of dropping large clams is incurred during the transport due to likelihood of losing the clam before it is dropped (D. Cristol, pers. comm.)

The age-related differences in foraging ability in this system are centered around prey size and profitability in terms of net energy gain. When young gulls learn efficient foraging skills, there are two main types of learning that occur. These are trial-and-error learning and observational learning, with trial-and-error learning being the most common of the two (Marchetti and Price 1989). In a system such as this, where the age-related difference has to do with the energetic reward gained from a particular prey item, trial-and-error learning is the most likely explanation for the development of prey assessment abilities. Herring gulls do not appear to be born with a complete set of prey selection criteria for foraging drops since yearlings lack the prey selection abilities of more experienced gulls. Therefore, young gulls must drop both profitable and less profitable prey in order to learn that smaller clams are less profitable.

Foraging patch selection did not account for the differences in prey size dropped by yearling and older gulls. All age classes of gulls concentrated their foraging efforts in the higher quality patches. Yearlings were simply choosing high and low quality clams when in these high quality patches. Since yearling gulls are unable to assess an individual clam as more or less profitable, it is very unlikely that they would be able to assess patch quality based on the frequency of profitable-size clams. However, yearling gulls still foraged in the more profitable patches. This suggests that if the proportion of profitable clams in an area is important in choosing a foraging area, yearlings are probably foraging in the areas where the older gulls are foraging rather than assessing foraging patches themselves. However, overall clam density may be more important than the proportion of profitable clams, in which case younger gulls may very well be choosing foraging patches on their own. Regardless, foraging patch selection does not vary with age and further studies on the criteria for patch selection are needed to answer these questions.

It has been suggested that the response of dropping an object with a hard exterior is an innate response to the hard covering (Tinbergen 1960). While dropping may be an innate response, I found anecdotal evidence that suggests observational learning could play a role in the development of prey dropping behavior even at a very young age. During the summer of 1999, I visited potential drop sites along the Eastern Shore of Virginia before newly hatched chicks were able to leave the colony. I visited these sites, primarily boat launches, bi-weekly as far south as Oyster, VA and as far north as Chincoteague Island, VA. I swept all concrete surfaces until they were cleared of shells and debris. On subsequent visits, I looked for evidence of smashed clams or other mollusks prior to re-sweeping the surfaces. Out of eleven potential drop sites, I found evidence of dropping occurring at seven of these sites. Furthermore, at three of these seven sites, I observed herring gulls dropping clams (*Mercenaria mercenaria*). Prey-dropping behavior was observed at boat launches in Wachapreague, Oyster, and within close proximity to a herring gull colony along the causeway to Chincoteague Island. This is certainly not conclusive evidence that prey dropping behavior is developed through observational learning. However, it does suggest that yearling gulls may observe clam dropping behavior before they can even fly, and thus, even "naïve" yearlings may have had some relevant experience by the time they had arrived at my study site in November.

Future studies on these gulls should examine the actual selection and number of rejections occurring when gulls pluck clams from the mud. Wedge clams are buried underneath the mud with very few apparent surface cues identifying their location. Herring gulls of all ages seem to have no problems locating clams, however. It would be interesting to investigate how much information the gulls are gaining from whatever surface cues they are using. In other words, is a gull able to determine the size and profitability of a clam while it is still buried in the mud? Further inquiries into the energetics of the prey drop might also prove worthwhile. While I found no differences in drop height with age, other energetic aspects such as age-related differences in time spent in the air flying to the drop site, likelihood of theft and harassment and substrate selection might all reveal further differences in foraging efficiency with age. Finally, as caloric profitability varies by clam size, so does a clam's breakability. Smaller clams require lower minimum heights in order to smash them open, but contain fewer calories. Large clams require greater heights in order to smash them open and contain more calories than small clams. Since experienced gulls are able to assess clam size to some degree and choose more profitable clams, it is possible that they could also adjust their drop height depending on the size clam being dropped. Because of the difficulty in separating a gull from its valuable prey, I collected only a limited amount of data on drop height by clam size and results were inconclusive due to small sample sizes. The tentative conculsion that gulls of all ages drop the same sizes of clam and that they do not change drop height as they gain experience should be treated with caution, with further investigation warranted.

APPENDIX A

Herring gulls can be rapidly and reliably aged in the field due to their distinct plumages throughout the first four years of life. Since this study was conducted during the winter, only the basic plumages were used for aging individual birds in the field. Table 7 lists the important distinguishing body and plumage characteristics that were used to identify the age of a particular bird during data collection. It was also useful to describe the overall look of each age class of gull in basic plumage. A first year herring gull is, in general, an all dark brown or grey-brown bird. A second year herring gull resembles a paler first year bird with a noticeably lighter gray back and a whiter head with extensive streaking. A third year herring gull is a mostly white bird streaked with grey and brown, mostly grey mantle and wings with some brown present and dark spots on its tail feathers. A herring gull in adult basic plumage is a white-bodied gull with some dusky streaking about the head and uniform, pale-grey mantle and wings.

TABLE 7

BASIC PLUMAGES OF THE FOUR DISTINCT AGES OF HERRING GULLS

Age Class	1	2	3	4+
Head	streaked grey-brown with some white	white with extensive dusky streaks	white with dusky streaks	white with dusky streaks
Wings and Mantle	dark brown to grey-brown	brown with extensive solid grey	uniform pale grey with some brown on underwing and innerwing	uniform pale grey lacking brown markings
Tail	usu. grey-brown with dark bars and broad, blackish-brown subterminal band	whitish at base with broad, solid blackish subterminal band	white with highly variable dark subterminal markings	all white tail
Beak	uniform black, sometimes pinkish base	olive, drab or fleshy base with black distal tip	dull yellow with black or brown tip	yellowish with reddish or orangish spot on end of lower mandible
Legs and Feet	dark grey with flesh overtones	Pale pinkish buff	pale pinkish buff	pale pink or flesh colored

APPENDIX B

Table 8 gives preference scores for clam size classes 1 through 10. Preference scores are calculated using the following formula to determine how often a prey is chosen according to its level of abundance (Ivlev 1961):

$$\frac{p - q}{p + q}$$

The variable p in the above equation is the proportion of clams being consumed for a particular size class. The variable q is the proportion of clams found in nature for a given clam size class. Clam size classes that are avoided result in a negative preference score, while those that are preferred have positive scores. Preference scores that are closer to 1.00 indicate a higher degree of preference for that size class.

TABLE 8

PREFERENCE SCORES FOR CLAM SIZES 1-10

Size Class	% in mud	% on road	Preference Score
1	5.51%	0.04%	-0.982
2	19.97%	1.31%	-0.877
3	24.27%	5.13%	-0.651
4	17.04%	9.63%	-0.280
5	13.77%	23.89%	0.269
6	11.36%	21.82%	0.315
7	5.16%	25.16%	0.659
8	2.07%	9.91%	0.655
9	0.69%	2.96%	0.623
10	0.17%	0.07%	-0.445

This data is based on a sample of 581 clams collected in the mud in 1996-97 and 6045 clams collected along the road between 1996-99 by D. Cristol. The above preference scores are used in all calculations based on clam size preference throughout this study. Clams size classes of 7 and 8 have higher preference scores and are referred to as disproportionately dropped clam size classes.

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VITA

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