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## Suboptimal Foraging Behavior by Herring Gulls

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# **SUBOPTIMAL FORAGING BEHAVIOR BY HERRING GULLS**

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A Thesis Presented to

The Faculty of the Department of Biology of

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

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by

Jennifer R. Gamble

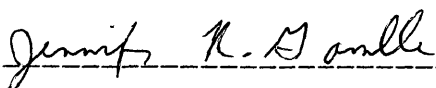
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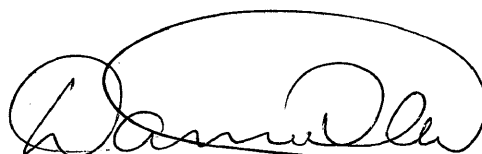
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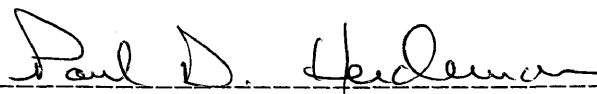


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Approved, August 2000



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## ABSTRACT

Optimality theory predicts that natural selection will have favored the behavioral alternative that leads to the greatest difference between benefit and cost of performing the behavior. I consider two behaviors of the Herring Gull, *Larus argentatus*, that appeared to be suboptimal alternatives to its typical foraging behavior. Gulls frequently drop clams onto hard substrates to break them open, but two modifications of this behavior occur: (1) dropping onto grass rather than a harder asphalt surface nearby (hereafter referred to as an off-road drop); and (2) dropping and catching the clam rather than allowing it to hit the ground (hereafter referred to as a drop-catch).

I tested five hypotheses for the off-road drop. I used experiments to test the propositions that (1) clams might open on grassy substrate without breaking or (2) that strong wind could blow clams onto the grass. I then conducted an observational study to further test the wind hypothesis and to test an additional three explanations: (3) the presence of other gulls on the road leads less competitive individuals to use a sub-optimal but less crowded grass drop site; (4) inexperienced juvenile gulls use the grass; or (5) the presence of automobiles causes gulls to drop their clams over grass. I observed Herring Gull dropping behavior on Jamestown Island, James City County, Virginia to determine the effects of wind, age, number of gulls nearby, and presence of automobiles on off-road dropping. I tested three hypotheses for the drop-catch with an additional observational study. The first hypothesis suggests that the drop-catch may be a form of object play in birds. Two alternative hypotheses explain this behavior as serving to reveal risk of theft or to reposition clams for more accurate dropping.

In my study of off-road drops, I concluded that the presence of vehicles causes grass-dropping, and that this effect may be influenced by the age of the gull. In my second study, I concluded that the drop-catch is an example of play in birds. The two alternative hypotheses were firmly rejected.

These two studies revealed that variations on the typical foraging drop, off-road drops or drop-catches, did not lead to a maximum net energy gain. Instead of rejecting the idea that evolution has shaped animals to behave efficiently, I conclude that my studies have revealed constraints on gull foraging not usually included in optimal foraging models.



## **SUBOPTIMAL FORAGING BEHAVIOR BY HERRING GULLS**

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Optimality theory predicts that natural selection will have favored the behavioral alternative that leads to the greatest difference between benefit and cost of performing the behavior. Thus, the animals we observe behaving today should exhibit optimal behaviors, such as efficient foraging. This thesis considers two behaviors of the Herring Gull, *Larus argentatus*, that appeared to be suboptimal alternatives to its typical foraging behavior. Gulls frequently drop clams onto hard substrates in order to break them open, but two modifications of this behavior occur: (1) dropping onto grass rather than a harder asphalt surface nearby (hereafter referred to as an off-road drop); and (2) dropping and catching the clam rather than allowing it to hit the substrate below (hereafter referred to as a drop-catch).

### **Prey Dropping by Gulls**

Herring Gulls are generalist carnivores with broad diets. Adults feed in many habitats, including dumps, harbors, and intertidal areas, on marine invertebrates, human refuse, eggs and young of other sea birds, insects, fish, and small mammals (Pierotti and Good, 1994). The exploitation of some of these prey items requires complex foraging techniques. Herring Gulls often select their prey based upon ease of handling; e.g., they prefer fish over squid and squid over shellfish. However, a shortage of preferred foods sometimes requires that they consume prey items that demand more time to process (Pierotti and Good, 1994). For example, on Jamestown Island in James City County, Virginia, Herring Gulls forage on *Rangia cuneata*, commonly called the wedge clam. Eating these hard-shelled clams requires several steps. To consume the edible interior a bird must locate the clam, pull it from the mudflat, properly orient and balance it in its bill, fly to an area of hard substrate, hover, drop, assess the condition of the shell, and, if necessary, redrop the unbroken clam (Tinbergen, 1961: 28-31; Richardson and Verbeek, 1986; Richardson and Verbeek, 1987).

## Prey Characteristics and Adaptations to Predation

Considering the amount of time and practice that may be necessary to perform a foraging drop efficiently, it might seem curious that a simpler technique is not used. It is the strength of the clam shell that makes the force applied by dropping necessary, and this strength is conferred by the composition and structure of the molluscan shell. Migrating vertically in the substrate may be a behavioral defensive strategy adopted by molluscs in response to predation, while thickening or strengthening the shell may be a physical adaptation to the same selective pressure. Modifications of the efficient foraging drop, such as an off-road drop, are even more baffling when the adaptiveness of the mollusc defenses are considered in greater depth.

An effective defensive strategy for clams is vertical migration in the substrate, such as that adopted by *Mercenaria mercenaria*. Though they engage in little horizontal movement, these clams move between depths of about 5 mm at high tide and 25 mm at low tide. Shorebirds such as Herring Gulls, because of their short beaks, usually feed within the top 20 mm of sediment. It might seem a better strategy for the clams to remain at depths greater than 20 mm at all times, but sediment clogs the siphons of permanently buried clams and prevents them from feeding efficiently (Roberts et al., 1989). This potential interference with filter feeding associated with being deeply buried entirely prevents some bivalve species from migrating to safety (Richards et al., 1999). In fact, when observed for long periods in captivity, *Rangia* does not seem to migrate at all, and in natural mudflats they are never found more than a few centimeters from the surface (personal communication, D. Cristol).

The thickness of *Rangia* shells may represent an alternative defensive strategy to burrowing. All molluscan shells are composites of organic and inorganic materials. This combination of proteins and minerals may reflect a defense against crushing. Other natural structures not subject to crushing, such as the pens of squids and the threads of spider webs, incorporate the same proteins but lack the minerals of the clam shell. Combining the two components of the molluscan matrix gives it a strength 3,000 times that of the mineral

crystals themselves (Belcher et al., 1996). The proteins in the matrix not only provide structure and strength, but also dictate which inorganic crystals will interact with the matrix and where those crystals belong. Only a particular structure and orientation of crystal will lower activation energy enough to allow a bond with a given protein to form. The specificity of the organic-inorganic bond is established by the organization of the matrix such that distinct structural, topographical, and chemical domains are produced across its surface (Mann, 1988; Weiss et al., 2000).

The shell of *Rangia* grows approximately 10 mm in length per year, reaching lengths of approximately 8 cm. Clam shells comprise three layers from inside to out: the inner complex crossed-lamellar or nacreous layer, the thin pallial myostracum, to which the mantle (extension of the body wall which secretes shell) is attached, and the outer crossed-lamellar or prismatic layer. The prismatic layer is composed of concentric first-order lamellae, parallel to the edge of the shell. Each first-order lamella is composed of second-order lamellae, which are arranged like shingles. Small, rod-like, crystalline third-order lamellae are joined at their sides to create the second-order lamellae. Growth is most evident in the prismatic layer because it occurs quickly in the spring and fall but slowly in the summer, resulting in differences in width of concentric first-order lamellae (Fritz et al., 1990). Having its proteins and crystals organized into these multiple, interwoven layers gives the shell additional strength and thickness.

While thickening the shell may effectively defend a mollusc against a shell-crushing predator, this strategy will not be effective against a shell-dropping predator. Shell modifications necessary to defend a clam against crushing are different from those necessary to defend a clam against striking pavement. In addition, selection may never favor adaptations against dropping because a thick-shelled, gull-dropped mollusc that did not crack open when dropped on a rock would still be stranded and therefore die anyway. Only when some of the prey survive the predator's attack can resistance to predators evolve (Blundon and Vermeij, 1983). Therefore, if *Rangia*'s shell thickness is a defensive strategy, it is likely to have evolved in response to a predator tactic other than prey-dropping.

## Optimal Foraging Theory and its Relation to Clam-Dropping

While *Rangia* shells have not become thick in response to gull predation, the tactic of dropping prey is likely an adaptation by the gull to the crush resistant traits of the shell. Just as the clam shell is shaped by natural selection, so too should be the predatory drop used by gulls to crack the clam shell. Prey-dropping by birds may be studied in the context of optimality theory, a tool used to understand particular examples of adaptation by helping to identify the forces and constraints that have influenced the adaptation. The aim of an optimality model is to understand the range of possible solutions, or adaptations, to a biological problem. When predictions based on optimality are not met by an animal's behavior, insight is gained into the selective forces and constraints that may be acting on that animal (Kamil, 1983; Parker and Smith, 1990).

Optimality theory is particularly useful in studying foraging behavior since the energy gained from this activity is easily measured and the decisions to be made by the animal are readily identifiable. Simple optimal diet selection models assume that: (1) animals maximize the average rate of energy intake over the long term, (2) searching and exploiting are mutually exclusive, and (3) the prey population is randomly dispersed (Ward, 1991). With regard to optimal predatory dropping, a gull must choose an appropriate size of clam, hardness of target substrate, height from which to drop the clam, and number of times to drop it (Richardson and Verbeek, 1987). This is not meant to imply an awareness on the part of the gull that it is acting optimally. Evolution may select for simple behavioral rules that govern an animal's seemingly-complex foraging behavior and lead to a match with the theorist's predictions (Shettleworth, 1998). An optimality model of avian prey-dropping predicts that foraging drop height should decrease with an increasing risk of loss to another Herring Gull, i.e. when more individuals are present at the drop site (Switzer and Cristol, 1999). Further, since clams have the same probability of breaking regardless of the number of times they have been dropped (Cristol and Switzer, 1999), they should be dropped from a constant height when repeatedly dropped. In addition, the model predicts that gulls foraging in an area with a variety of dropping

substrates that differ in hardness should choose harder substrates and drop clams from lower heights when over harder substrates. Finally, since all gulls feed on the same type of clam, and these clams vary in breakability depending on size (unpublished data, D. Cristol), optimum drop height should be a function of size (Switzer and Cristol, 1999).

Several steps are involved in using optimality theory as a tool with which to analyze behavior. First, a question must be posed with regard to the behavior of an animal, e.g., why do Herring Gulls occasionally drop clams on grassy substrates? Second, a set of plausible (given biological constraints) alternative strategies must be proposed, e.g., dropping exclusively on grassy substrate or dropping exclusively on hard substrate. Third, an assumption about the measure of Darwinian fitness being maximized, such as rate of energy intake, should be made. Fourth, the fitness payoff of each strategy should be assessed using assumptions about the costs and benefits of components of that strategy (Parker and Smith, 1990). In the case of the foraging gulls, one might develop an equation similar to that used in a study of clam foraging by Kelp Gulls (*Larus dominicanus*). Clams were burned to measure the gross energy content of each size class. The energy cost of prey consumption was then determined using handling time (time taken to crack a clam), assimilation efficiency, basal metabolic rate (BMR), and multipliers of BMR for flying, searching, and other parts of the handling process (Ward, 1991). The final step in using optimality theory involves testing the predictions made by the optimization model against the observations.

If the predictions of the model match the observations, the forces shaping this strategy may have been properly identified. If not, this strategy may not be adaptive. Alternatively, assumptions made about the plausible strategies, the measure of fitness being maximized, or the costs and benefits of a particular strategy may be inaccurate. In other words, using this equation to determine that dropping exclusively onto a road yields the highest rate of energy gain may suggest that this behavior is not adaptive. Alternatively, this discovery may indicate that the researcher has not recognized an important factor influencing this behavior, such as the energy expended in competing for a drop site on the road. This example illustrates that optimality theory is a tool which may be used to

understand behavior rather than a proposition, as some believe, that animals should always be found to act optimally (Parker and Smith, 1990).

Predictions made by optimal foraging theory based on the assumption that animals are maximizing energetic efficiency have been supported by studies of various prey-dropping birds. In the study, mentioned above, of optimal foraging on clams by Kelp Gulls, the birds were found to select clams of a size that ensured net energy gain (Ward, 1991). Herring Gulls along a tidal flat area of the Dutch Wadden Sea dropped only large mussels (*Mytilus edulis*) and American Razor clams (*Ensis directus*) despite the fact that the clam population was a bimodal distribution of small and large individuals (Cadee, 1989). Northwestern Crows (*Corvus caurinus*) were shown to maximize energy gain in their selection of drop height and snail size (Zach, 1978, 1979). Similarly, American Crows (*Corvus brachyrhynchos*) demonstrated efficiency in prey-dropping with walnuts. They dropped walnuts with harder shells from greater heights, used greater heights when over softer substrates, decreased drop height when more potential thieves of prey were present, and decreased drop height with repeated drops of an individual walnut, as predicted by the fact that walnuts weaken with each drop (Cristol and Switzer, 1999).

Though used in many optimality models, energetic efficiency is only one ultimate factor that may control the foraging behavior of an animal. Making an incorrect assumption about the currency, or measure of Darwinian fitness, that is being maximized by a behavior can lead to a mismatch between an optimality model's predictions and a researcher's observations (Charnov, 1976). Several species of geese, for example, eat small, empty clam shells and pieces of shell. In terms of gaining calories, this behavior seems suboptimal. However, this behavior may reflect a nutritional requirement rather than an energetic one since it allows female geese to gain scarce calcium prior to egg-laying. Male geese engage in this behavior as well but to a lesser degree, suggesting that the shells may also be used as grit (Flint et al., 1998). It is important to note that caution is warranted when labeling a behavior suboptimal on the basis of its apparently wasting energy.

Whether or not natural selection can optimize behavior depends on the rate at which selection can alter genes, the amount of genetic variance and gene flow, the rate at which

environmental conditions change, and random effects on populations like genetic drift. The presence of variation in populations does not discount selection's ability to optimize. Some amount of variation may be maintained by selection because of changing conditions. For example, the strategy of dropping over grassy substrates may have been maintained because populations occasionally exploit areas with few patches of hard substrates. Alternatively, variation may be selectively-neutral, i.e., selection may not act strongly enough in the immediate area of the adaptive optimum to exactly target that optimum (Parker and Smith, 1990). For example, selection may only have the capacity to ensure that gulls often, rather than always, drop over hard substrates. The off-road and drop-catch behaviors that I studied seem to be such extreme deviations from normal foraging behavior that they could not immediately be described as adaptive variations. This is because both behaviors seemed to result in a complete failure to obtain any food despite considerable costs. They must be viewed as sub-optimal until a satisfactory explanation can be accepted that demonstrates an adaptive function for either or both.

### **Variations of the Foraging Drop**

Knowing that natural selection has shaped the gulls' foraging drop to effectively crack open clams, it is difficult to understand why Herring Gulls would vary this drop in any way. This study investigated two variations of the typical Herring Gull foraging drop described previously. I observed both variations while studying winter foraging of Herring Gulls. My first chapter examines the dropping of clams into the grass bordering the road that leads out to Jamestown Island. It would seem that a gull would always benefit by dropping its clam onto a hard substrate such as the road, and my preliminary observations indicated that they frequently did so; indeed the road is littered with broken clam shells. However, while some previous studies support this observation that Herring Gulls can selectively drop on hard substrates (Ingolfsson and Estrella, 1978; Beck, 1982), some older studies have reported that they drop on soft and hard substrates, concluding that they are non-selective (Tinbergen, 1961: 28-31; Oldham, 1930). I believe that these



studies are not mutually exclusive; it is my impression that Herring Gulls can drop selectively over hard substrates, but that under certain conditions off-road dropping occurs. Therefore, I decided to look for common factors of the off-road drops, such as the age of the dropper or weather conditions, that might reveal a reason for the performance of this unusual behavior by some gulls. I proposed five hypotheses to explain this behavior. The first is that clams may open without the shell breaking when dropped on the grass, presumably through stunning; i.e., the grass is just as suitable a foraging substrate as the road. The second is that gulls do not make allowances for wind, so clams are blown onto the grass during periods of high wind. The third is that only young birds, which have not yet learned to forage efficiently, are responsible for the off-road dropping. The fourth is that benefits gained by using the hardest available substrate, the road, may be outweighed by the costs of competing for that drop site when other gulls are present, making the use of a softer substrate, the grass, advantageous for less-competitive individuals. The final hypothesis is that gulls drop onto the grass in response to approaching automobiles.

My second chapter examines another type of drop distinct from the typical foraging drop. Rather than dropping a clam onto a hard substrate, Herring Gulls occasionally dropped clams and then swooped down and attempted to catch them. This behavior was sometimes performed with objects other than clams. Gulls sometimes performed this drop-catch behavior several times in a row. One of my hypotheses to explain this behavior is that it is an example of play in birds. This behavior has been described as play in Herring Gulls as well as in other species of birds. However, other studies of the drop-catch in birds have mostly been anecdotal and have not tested alternatives to the hypothesis that it is play (Wheeler, 1943; Negro et al., 1996; Pandolfi, 1996; Beck, 1982; Terry, 1990; Graham, 1988; Warden, 1982; King, 1970; Sauer, 1978; Humphreys, 1964). In Chapter 2, I investigate this possibility as well as the alternatives that drop-catch behavior is used to prevent theft of prey or that this maneuver is performed to reposition the clam for a better dropping orientation.

## CHAPTER 1

During a preliminary study of winter foraging by Herring Gulls on Jamestown Island in Virginia, I regularly found whole *Rangia* clams in the grass beside the asphalt road leading out to the island. This seemed to violate the predictions of optimal foraging theory, which suggest that birds should drop over the hardest available substrate (Switzer and Cristol, 1999). Using a hard substrate would result in a gull's flying the shortest vertical distance (number of drops times height of each drop) to crack the clam's shell. Natural selection should have favored behavior leading to this energetic efficiency. If a soft substrate required much less flight, because a hard substrate was farther away, then it might be more profitable to drop on the soft substrate. However, in the case described here, the grass and road drop sites were at the same location, both far from clam-gathering areas. Clams dropped on grass were mostly unbroken, and many of them were too far from the road to have bounced there following a drop onto the road. They were too scattered to have been the middens of otters, raccoons, or muskrats. Further observation confirmed that Herring Gulls were dropping the clams onto the grass, despite the fact that I had many times observed their using the road as a dropping substrate without error. In addition, even though there is more grassy substrate than paved substrate, the amount of road is large; the section leading from the mainland to Jamestown Island is  $4800 \text{ m}^2$ , while the mowed grass bordering the road is  $32,000 \text{ m}^2$ . The objective of this study was to test five hypotheses to explain this apparently sub-optimal off-road dropping behavior.

The first explanation for the off-road drop, the Stun Hypothesis, is that gulls use the grass because it is just as suitable a foraging substrate as the road. Some bivalves, if dropped from an adequate height onto a soft substrate, may open without the shell breaking, presumably through stunning. In addition, some molluscs have been reported to break open on substrates softer than rock (Kent, 1981; Ingolfsson and Estrella, 1978). In order to test whether or not *Rangia* become stunned and open when dropped on a grassy substrate, I performed an experiment in which I dropped clams onto grass and tested whether they cracked or became easier to open.

The Wind Hypothesis is that dropped clams are blown onto the grass by high winds. Foraging gulls, which track wind activity closely, are likely to fly during these periods of high wind because they can gain extra lift and thereby reduce energy expenditure when transporting clams (Haney and Lee, 1994; Fritz, 1998; Gilchrist and Gaston, 1997). In addition, gulls often fly against strong headwinds, possibly in an effort to steady their flight and enhance prey detection (Spear, 1997). Gulls maintain a constant drop height over varying wind speeds, but may compensate in other ways, for example, by hovering longer before dropping in higher winds (Beck, 1982). I conducted an experiment to determine the potential horizontal displacement of a falling clam with various combinations of wind speed, drop height, and clam size. The Wind Hypothesis predicts that gulls will drop clams onto the grass more often during periods of high wind than periods of low wind because clams dropped over the road will be displaced far enough by wind that they end up on the grass.

The Experience Hypothesis is that only young gulls drop clams onto the grass, since they have had insufficient time to perfect foraging skills through practice. Either they are indiscriminate with regard to the hardness of the substrate below them, or their aim is worse than that of adults. Young animals frequently forage suboptimally because they have not yet gained necessary information about their environment and prey through experience (Kamil, 1983). I analyze the relationship between age and the rate of off-road dropping because the ability of a gull to perform a complex foraging task may vary with age. A lack of efficiency in complex foraging has been noted in several species of juvenile gull. For example, while all adult Western Gulls (*Larus occidentalis*) drop clams, only about half of the juveniles do. Younger gulls that drop do so more times and from lower heights than adults, and they do not adjust height to account for clam weight as do the adults (Maron, 1982). Juvenile Herring Gulls have been shown to forage less efficiently than adults for prey items that require complex processing. During the first four years of their lives, young gulls gradually learned and perfected skills necessary for refuse extraction from dumps, such as digging for, recognizing, and extracting edible items (Greig et al., 1983; Verbeek, 1977a). Young Herring Gulls, as well as Bonaparte's Gulls,

*L. philadelphia*, and Ring-billed Gulls, *L. delawarensis*, plunge-diving for fish and starfish gradually improved in their ability to detect, to judge the suitability and accessibility of, and to carry prey items. By their fourth year, these young gulls fed nearly as successfully as adults and relied less on chasing and stealing for food (MacLean, 1986; Verbeek, 1977b). As an additional example, yearling Herring Gulls, as well as Kelp Gulls and Glaucous-winged Gulls, *L. glaucescens*, feeding on shellfish dropped them a greater number of times, more often over soft substrates, and from a wider range of heights than adults, and were, in the opinion of the researchers, more likely to drop their clams accidentally (Siegfried, 1977; Ingolfsson and Estrella, 1978; Barash et al., 1975). Through these studies it can be seen that several factors are involved in performing a complex foraging task efficiently, whether the task is prey-dropping or digging for refuse. Juvenile gulls must learn and improve foraging skills as they mature. Therefore, age-related inefficiency could explain the off-road drop.

Proposing that young gulls perform off-road drops because they cannot yet forage efficiently implies that adult gulls do preferentially drop over hard substrates, which may seem obvious but has been demonstrated conclusively only in crows. Some older studies claimed that crows foraged discriminately over hard substrates but that gulls did not (Oldham, 1930; Tinbergen, 1961: 28-31). A more recent study demonstrated that juvenile gulls accounted for most of the soft-substrate dropping observed within a population of foraging gulls (Barash et al., 1975). Others have stated that gulls are unquestionably capable of choosing hard dropping substrates, although relative areas of hard and soft substrate were not measured (Siegfried, 1977; Goethe, 1958; Ingolfsson and Estrella, 1978; Beck, 1982). Gulls at Jamestown Island target the road in their foraging drops significantly more often (83 % of 504 drops) than would be predicted by chance given the amount of hard substrate (3.9 % road and rock) versus soft substrate (96.1 % water, mud, and grass) available ( $\chi^2 = 636.7$ ,  $df = 1$ ,  $p < 0.0001$ ). Gulls may learn gradually to target the road, though, and the Experience Hypothesis predicts that younger birds should drop onto grass more often than adults. Wind speed and direction may exacerbate this inefficient dropping behavior, but younger birds are predicted to be less efficient than older gulls

under any wind conditions.

The Competition Hypothesis is that competition exists for the optimal dropping substrate, the road, so some gulls escape competition by dropping on the grass. In keeping with this idea, subordinate Herring Gulls fed in suboptimal parts of a garbage dump when the degree of competition from dominant birds was higher in a more optimal part (Monaghan et al., 1986). Glaucous-winged Gulls defended particular areas of rock used as drop sites in Washington (Barash et al., 1975), so it is possible that areas of road were defended. This hypothesis predicts that a lower proportion of clams will be dropped into the grass when fewer competitor gulls are present. If juvenile gulls as a group tended to be the subordinate gulls, then the Competition Hypothesis would make the same prediction as the Experience Hypothesis, that the young gulls would do most of the off-road dropping. However, I assumed that juveniles were not necessarily the same birds as the subordinates because: (1) juvenile Herring Gulls are significantly more likely than adults to attack in order to displace an actively-feeding bird; (2) juveniles are just as likely as adults to actually displace a feeding bird; and (3) juveniles are just as capable as adults of winning attacks in defense of their food (Greig et al., 1983). Thus, the Competition Hypothesis does not predict that juveniles will account for a disproportionate number of off-road drops, but instead that the subordinate segment of the population will.

Finally, the Automobile Hypothesis is simply that gulls may drop their clams in the grass in response to approaching automobiles. Perhaps fear outweighs their feeding motivation, causing them to release the clam as they escape the automobile. Distraction by the automobile could have the same result. Crows have been shown to avoid cars when using roads as surfaces for breaking walnuts, although they did not drop walnuts or leave them unretrieved when they fled from oncoming vehicles (Cristol et al., 1997). If this hypothesis is correct, gulls should drop clams onto the grass primarily in the presence of oncoming cars.

## METHODS AND RESULTS

### **Determining whether gulls were responsible for clams in the grass**

#### Methods

To determine if off-road dropping, which was not witnessed frequently, occurred regularly, I conducted an off-road clam survey. On 19 January, 2000, three 14 X 14 m sections of grass were marked along both the east and west sides of the road leading across the constructed isthmus to Jamestown Island. These sections were initially cleared of whole clams and shells and then surveyed on 9 February, 1 March, and 22 March, 2000, for newly-appearing whole clams and matching unbroken valves found within 0.5 m of each other. Each section was surveyed for 14 minutes each time. Four poles marked the corners of each section and a 14-m length of string was laid down parallel to the road and 1 m from the edge of the section to delineate a 14-m X 1-m swath for collecting. Once this swath had been surveyed from north to south and back again the string was moved closer to the road by 1 m, delineating a new swath. This was repeated until the entire section was cleared.

For each clam collected, I recorded size (usually 2.5 - 8 cm from the left to right side of one shell) to determine whether a specific size was being dropped in the grass. For example, if only the smallest clams were found in the grass, this would lend support to the Wind Hypothesis. For each clam, I recorded whether the clam was <1 or >1 m from the road, because clams within 1 m may have bounced from the road rather than being dropped into the grass.

#### Results

During the two survey dates following the initial clearing, several clams of various sizes were collected from both sides of the road at distances greater than 1 m (Table 1).

**Table 1. Clams collected during off-road surveys.**

<b>Date</b>	<b>Total OR clams</b>	<b>East side</b>	<b>West side</b>	<b>0-1 m</b>	<b>1-14 m</b>	<b>Size (cm)</b>
2/9	5	5	0	0	5	5.0 - 5.7
3/1	8	3	5	1	7	4.3 - 6.8
3/22	0	-	-	-	-	-

This confirms that new clams were regularly appearing in the grass. The observational study below confirmed directly that Herring Gulls were dropping clams on the grass. On the final survey date, no clams were collected. By this date, the gulls had ceased dropping clams altogether and had migrated away from the site, further supporting the conclusion that gulls were the source for clams dropped on the grass.

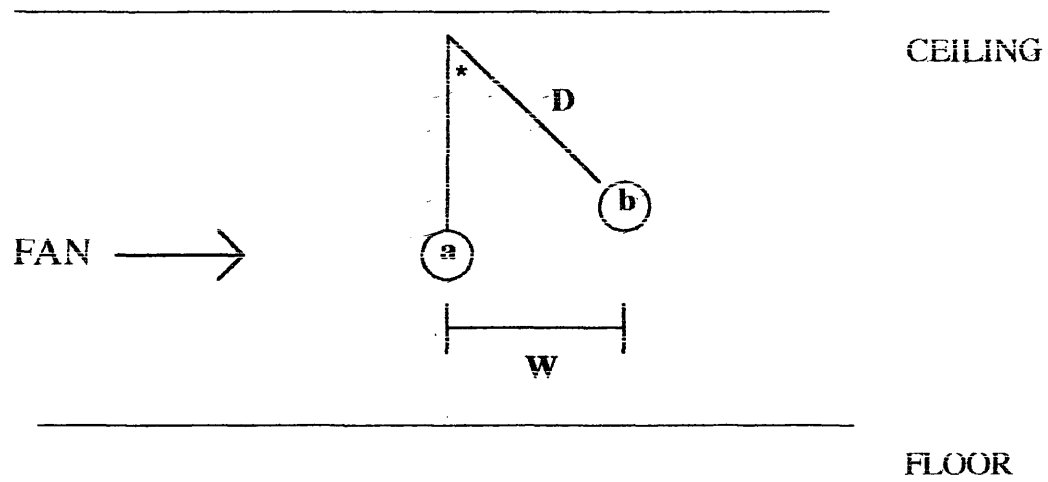
### **Determining whether wind could blow clams into the grass**

#### Methods

To determine whether the winds occurring at Jamestown Island could blow into the grass clams that had been dropped over the road, I used a wind simulator to test how far suspended clams could be deflected. I performed this experiment with both a large (6.7 cm from left to right side of valve) and a small (3.1 cm) clam. To do this I suspended a clam from the ceiling of a room. Two strings were attached, using duct tape, to the left and right side of one valve of the clam (rather than one string attached to the center of the valve, which would have allowed spinning). The umbo (the bulge at the hinge of a clam) was oriented downward. A fan was situated 61 cm from the untaped valve. A strip marked off in centimeters was situated beneath the clam and extended away from the fan in the direction of the wind path in order to measure horizontal displacement of the clam (Fig.1).

The fan was then turned on and adjusted to a desired speed using a rheostat and a digital anemometer (Ultimeter 100). Using the anemometer I determined the wind speed at the exact spot where the clam would hang. The speed was recorded as the initial speed. Once the desired speed was set, the clam was placed in the path of the wind and allowed thirty seconds to reach equilibrium position. The horizontal displacement of the clam was then recorded, if the clam became stationary. If the clam oscillated, the mean of maximum and minimum displacements was used. This procedure was performed twenty times for each of four wind speeds representing the range of wind speeds I recorded at Jamestown Island: 0, 10, 20, and 25 km/h.





**Figure 1.** Diagram of components used in determining whether wind could blow clams into grass. a = original position of clam; b = clam at equilibrium at a particular wind speed; W = horizontal displacement of the clam; D = string length; \* = THETA = angle of displacement.

The horizontal displacement values (W) and the vertical hang distances (D) were then used to compute the angle from vertical of a clam's fall at a particular wind speed, using the formula  $\text{THETA} = \arcsin W/D$  (Fig. 1). Using this angle and the range of heights of a typical gull drop, which was 3-10 m (unpublished data), the potential horizontal displacement of clams dropped by gulls was determined with the formula:

$$(\tan \text{THETA}) \times \text{height} = \text{potential horizontal displacement (W)}.$$

### Results

Wind speeds in the range recorded on Jamestown Island moved the large clam very little from its vertical hang path. At a wind speed of 25 km/h, the large clam was displaced at an angle of 3.25 degrees from vertical (Table 2). Dropping for 10 m at this high wind speed, a large clam would be horizontally displaced by only 0.57 m (Table 3). At a wind speed of 25 km/h, the small clam was displaced at an angle of 6.49 degrees from vertical (Table 2). Even dropping for 10 m at a high wind speed, a small clam would be horizontally displaced by only 1.14 m (Table 3).

### **Determining whether clams could open on grassy substrate without breaking**

#### Methods

To determine whether clams could be opened more easily after being dropped on grass, I simulated the event with one group of clams and tested whether they could be opened more easily than a control group that had not been dropped. I collected 36 clams (18 large [5.7 - 8 cm] and 18 small [2.7 - 4.3 cm]) gathered from the mudflat at Jamestown Island at low tide on 13 February, 2000. The clams were transported in 15 cm of mud in a 32-l ice chest to an outdoor processing area. I manufactured handles on both valves of

**Table 2. Determination of angle at which wind can displace a falling clam.**

Clam size (m)	Wind speed (km/h)	W (m)	D (m)	THETA (degrees)
0.067	10	0.03	2.29	0.75
0.067	20	0.1	2.29	2.5
0.067	25	0.13	2.29	3.25
0.031	10	0.04	2.3	1
0.031	20	0.15	2.3	3.74
0.031	25	0.26	2.3	6.49

W = average horizontal displacement of clams; D = average distance from ceiling to clam;

THETA =  $\arcsin(W/D)$  = angle from vertical of path of wind-blown clam.

**Table 3. Predicted horizontal displacements for clams dropped from heights used by gulls on Jamestown Island.**

<b>Clam size</b>	<b>Wind speed</b>	<b>Height</b>	<b>THETA</b>	<b>Predicted W</b>
<b>(m)</b>	<b>(km/h)</b>	<b>(m)</b>	<b>(degrees)</b>	<b>(m)</b>
0.067	10	3	0.75	0.04
0.067	20	3	2.5	0.13
0.067	25	3	3.25	0.17
0.067	10	10	0.75	0.13
0.067	20	10	2.5	0.44
0.067	25	10	3.25	0.57
0.031	10	3	1	0.05
0.031	20	3	3.74	0.2
0.031	25	3	6.49	0.34
0.031	10	10	1	0.17
0.031	20	10	3.74	0.65
0.031	25	10	6.49	1.14

THETA = angle from vertical of path of experimentally wind-blown clam; Predicted W = predicted horizontal displacement of a clam dropped by a gull on Jamestown Island = (tan THETA) times height of drop.

each clam, which I later used in attempting to pull the clams apart. To attach these handles, mud was first removed from the surface of each clam using tap water, a rough sponge, and paper towels for drying. Clams were then arranged in a row. Each valve of each clam was abraded 30 times using coarse grit sandpaper. Seventy-two 15-cm lengths of cotton clothesline were cut and 2.5 cm of each end of each length were frayed. Epoxy (Ace 60-second) was used to attach both ends of one segment of clothesline to one valve of each clam, forming a U-shaped handle for pulling. Pressure was applied to the ends of the clothesline for 60 seconds to set the glue. This was repeated for the following three clams in the row. The first four clams in the row were then flipped over and treated in the manner of the first valve, having U-shaped segments of clothesline attached to them. This was repeated for the remaining clams, four at a time. Gluing was done in increments like this so that the freshly-mixed epoxy would not harden before being applied to the clams.

After allowing the epoxy to dry for one hour, one segment of clothesline on each clam was labeled control or experimental, alternating down the row of clams. Experimental clams were dropped and then pulled upon, while control clams were pulled upon without having been dropped. Each experimental clam was dropped from a height of 8.5 m onto a grassy surface with its umbo oriented down. Immediately after the drop, one loop of clothesline was attached to a buried hook; the other loop was pulled upward with a hand-held scale (Hanson 100-lb.). The greatest force reached before the glue or the clam gave way was recorded. The preceding two steps were then performed with a control clam (which had not been dropped), alternating between treatments. The total amount of time that passed from collection of live clams to last drop was 10 h.

## Results

In all cases but one, pulling resulted in ripping the clothesline from the clam rather than in opening the clam. The forces reached ranged from 1 to 30 lbs (mean  $\pm$  SD = 8.11  $\pm$  6.05 lbs, n = 36). One small control clam was pulled open using 13 lbs. of force. However, no other clams opened, even with manual manipulation of the clams following

the pulling procedure. There was no significant difference between the amount of force applied to control and experimental clams (mean force: experimental = 15.9 lbs, control = 21.1 lbs; Wilcoxon rank sum test,  $Z = 1.479$ ;  $p = 0.139$ ).

## **Factors influencing when gulls drop clams on grass**

### Methods

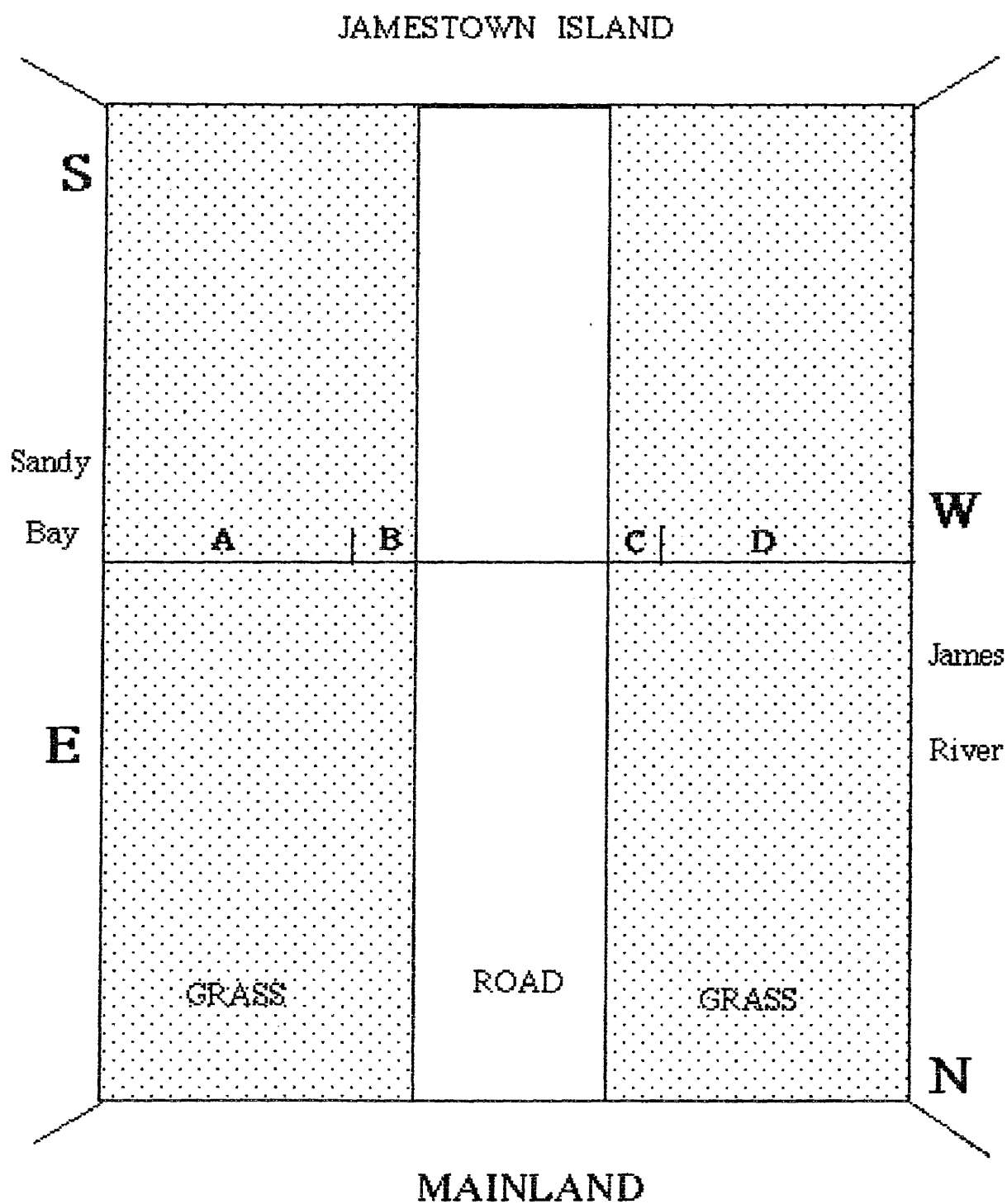
To test the Experience, Competition, and Automobile hypotheses, I observed gulls dropping clams under conditions in which experience, levels of competition, or presence of automobiles varied. Data were collected from Sandy Bay, east of the isthmus road to Jamestown Island, where numerous species of shorebirds and waterfowl forage, including five species of gulls. During most low tides, extensive mudflats east of the road are exposed, allowing access to *Rangia* clams, upon which both juvenile and adult Herring Gulls feed.

Herring Gull dropping behavior was observed for a total of approximately 30 h over 20 d for 1-3 h / day before low tide from November to April in 1998/99 and 1999/2000. At the beginning of each observation period, I first recorded date, time of day, and tide level. I then recorded wind speed and direction using the Ultimeter 100 weather station in order to determine the relationship between off-road drops and this environmental variable. These values were later lumped into 5-km/h categories, which provided approximately equal sample sizes for each category of wind speed. I updated wind speed and direction data every 15 min. I recorded the age and number of Herring Gulls present every 30 min. Since passage of a raptor caused gulls to leave the area for approximately 15 min, creating a gap in the feeding data, I noted the presence of eagles or hawks throughout each observation period.

The recording of each data point began with a gull acquiring a clam and ended with loss or consumption of the clam. I recorded the type of drop (Drop, Drop-Catch, or Abandon) to allow later comparison of the characteristics of each type. Numbering each

drop in a drop series performed by one gull allowed me later to select only one drop per series to avoid this source of pseudoreplication. Recording the fate of the clam (abandoned, lost, stolen, or eaten) allowed me to discern any differences between the outcome of an off-road drop versus a foraging drop. I determined gull age by the color of the plumage, which is distinctive in first- through fourth-year gulls (Pierotti and Good, 1994), thus allowing me to test the relationship between age and off-road dropping. Using the designations in Figure 2, I recorded substrate and, if grass, distance from road where clam struck, in order to document off-road dropping. I recorded all gulls within 5 m of the drop site as being other gulls present at drop site, allowing me to examine the effect of competition on off-road dropping. Finally, I recorded a car as being present if the car and the gull were simultaneously within a 30-m radius of the drop site. This information was used to investigate the relationship between off-road drops and the presence of automobiles.

Results are presented as number of off-road drops divided by number of on-road drops seen under the same circumstances to control for changes in rates of feeding, numbers of gulls, or other factors that might affect the absolute number of off-road drops observed. Groups were compared using Chi-square tests. Statistical power was calculated for non-significant results using a “small” hypothesized effect size of 0.05 (Cohen, 1969).



**Figure 2.** Diagram of substrate designations used in recording off-road drops. A & D = Grass 1, 1-14 m from road; B & C = Grass 2, < 1m from road.



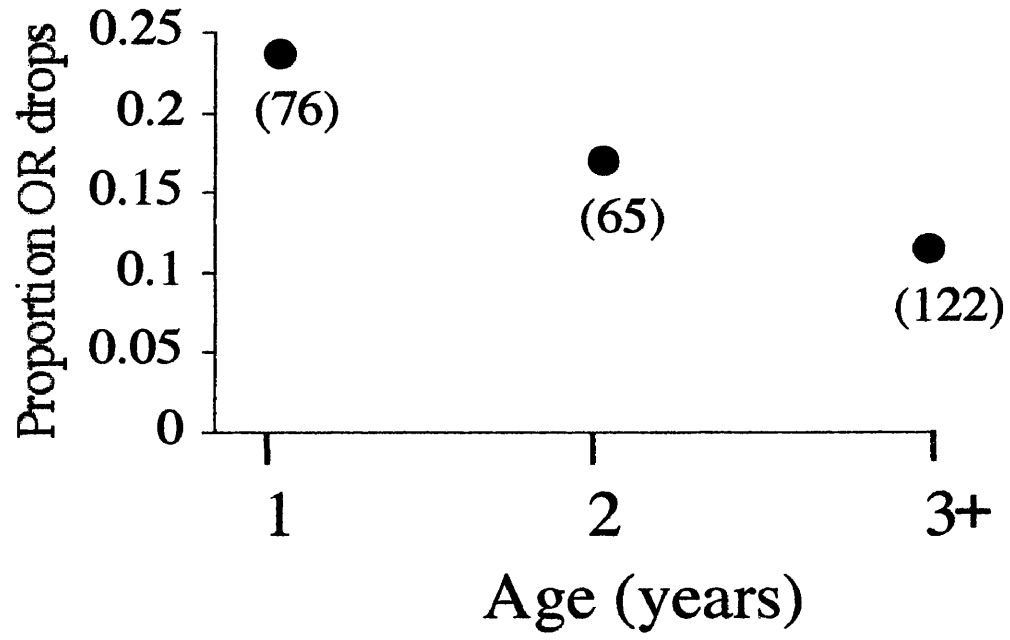
## Results

I tested the prediction of the Experience Hypothesis, that younger gulls would drop their clams on the grass more often than older gulls, by comparing proportion of off-road drops, relative to on-road drops, for each age. Consistent with the predictions of the Experience Hypothesis, a tendency towards a negative relationship was observed between the relative proportion of off-road drops and age (Fig. 3). However, the differences in relative proportions of off-road drops by age were not significant ( $X^2 = 5.1$ ,  $df = 2$ ,  $p = 0.077$ ; power = 90 %).

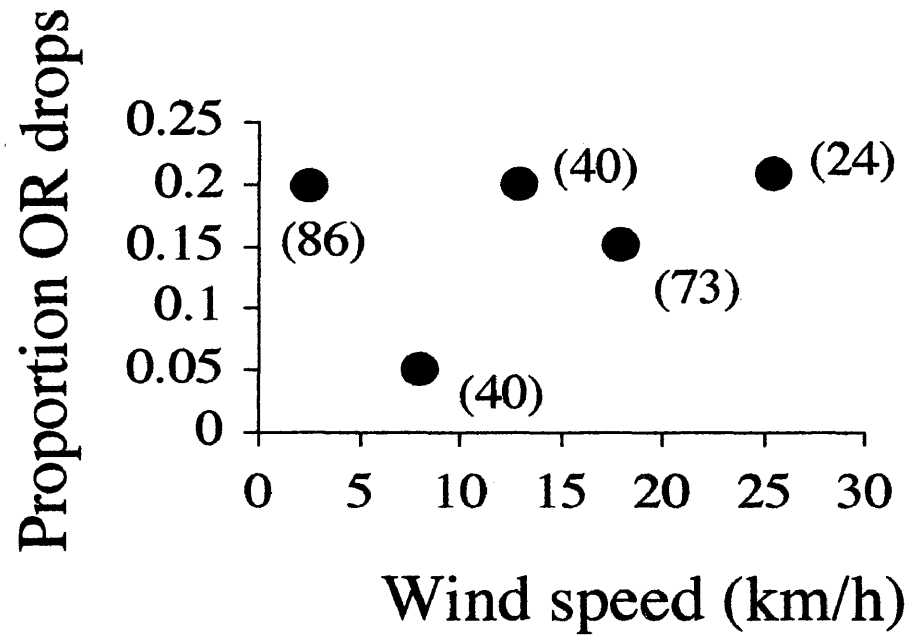
The Competition Hypothesis predicted that a more crowded drop site would cause some gulls to drop onto the grass. I tested this by comparing the proportion of off-road drops, relative to on-road drops, when there were or were not other gulls present. Off-road drops, relative to on-road drops, occurred as often when other gulls were absent (0.17,  $n = 122$ ) as when other gulls were present (0.16,  $n = 141$ ) ( $X^2 = 0.1$ ,  $df = 1$ ,  $p = 0.725$ ; power = 94 %).

The Wind Hypothesis would explain the presence of clams in the grass as the product of high winds that might blow clams off course after they were dropped over the road. Drops in the 21-25 km/h and the 26-30 km/h wind speed categories were combined due to low sample sizes in each. The data reveal no strong relationship between proportion of off-road drops, relative to on-road drops, and wind speed (Fig. 4). The differences in relative proportions of off-road drops by wind speed were not significant ( $X^2 = 5.3$ ,  $df = 4$ ,  $p = 0.255$ ; power = 82%).

Finally, I tested the prediction of the Automobile Hypothesis that approaching cars might scare or distract gulls, causing them to drop clams onto the grass. A higher proportion of clams was dropped onto the grass when cars were present (0.29,  $n = 31$ ) than when they were absent (0.15,  $n = 232$ ) ( $X^2 = 4.1$ ,  $df = 1$ ,  $p = 0.042$ ).



**Figure 3.** Relationship of off-road (OR) drops and age of gulls. Parentheses indicate sample sizes.



**Figure 4.** Relationship of off-road drops and wind speed. Parentheses indicate sample sizes.

## DISCUSSION

A few decades ago, gulls were labeled less intelligent than crows because they did not demonstrate as clear a preference for hard dropping substrates (Tinbergen, 1961: 28-31). Though comparison of animal intelligence has lost popularity, the issue of whether or not gulls are selective in their choice of foraging substrate remains unresolved. This study sought to explain the seemingly suboptimal clam-dropping behavior by Herring Gulls onto soft grass next to a hard road.

If I had shown that the bivalves upon which Herring Gulls feed broke open as easily on soft substrates as on hard, as suggested by the Stun Hypothesis, I would have had an easy explanation for the gull's unusual behavior. However, when I experimentally dropped clams on grass they were not more easily opened than control clams, thereby allowing me to reject the Stun Hypothesis. Alternatively, if I had found that strong winds blow clams off of their drop trajectories and onto the grass, as suggested by the Wind Hypothesis, I would have had an explanation for the presence of clams in the grass beside the road. However, by simulating wind and measuring clam displacement I showed that not even a small clam dropped from 10 m in 25 km/h winds could be blown more than 1 m off of the road, while clams were regularly found at a much greater distance from the road. Further, various sizes of clams were found off the road during the initial clam survey, indicating that this was not simply a case of unusually small clams being blown onto the grass. In addition, there was not a significant increase in the proportion of clams dropped on the grass during periods of higher wind.

The Competition Hypothesis explained the presence of clams in the grass as the result of less competitive gulls being excluded from the best drop sites. However, the proportion of off-road drops was no greater when other gulls were absent than when there were 1-18 gulls present. Another possible explanation, the Experience Hypothesis, suggested that only the juveniles would drop onto the grass because they did not have the skills to drop optimally. I found that young birds did not perform significantly more off-road drops than expected by chance. However, there was a tendency towards a negative

relationship between age and off-road drops.

In contrast to the other four hypotheses, the Automobile Hypothesis, that all gulls drop clams off of the road in response to approaching vehicles, was supported, albeit weakly, by the data. Herring Gulls performed significantly more off-road drops when an automobile was present (within 30 m of the drop site) than when none was present. Perhaps the motivation to avoid “predation” by the automobiles overrides the motivation to feed, causing the gull to release the flight-hampering clam. Alternatively, perhaps gulls are simply distracted by automobiles and release their clams as a result. This was a surprising result for several reasons. First, it has been suggested several times that birds drop hard food objects in front of cars so that they will be crushed without effort on the part of the birds (Maple, 1974; Grobecker and Pietsch, 1978; Conder and Everett, 1979). Second, during several years of casual observation I never had the impression that gulls responded to cars except to leave the road reluctantly just as the vehicle approached. Herring Gulls frequent human-disturbed habitats, cars are numerous at Jamestown, and the strictly-enforced speed limit (15 mph) allows birds to escape easily. Therefore, it seemed unlikely that the gulls would be frightened or distracted by the presence of a car. After investing so much energy into finding and transporting a clam, it seems very odd that birds would simply drop their clam onto the grass and leave it there because a car was approaching. Crows that were breaking walnuts by dropping them on roads in California also left the road as cars approached, but they took their walnuts with them (Cristol et al., 1997). In the future, the relationship between off-road drops, age, and automobiles should be investigated, although the sample size for drops in the presence of automobiles was too small to conduct this analysis in this study. However, first-year gulls do seem to drop on the road less often and on a rocky island isolated from cars more often than adults (personal observation), perhaps because they have not yet learned that the vehicles on Jamestown Island are likely to stop rather than hit them.

This study suggests that the off-road drop is not simply a random occurrence or mistake, but is connected to a specific environmental variable, the presence of automobiles, and perhaps to age as well. This provides insight into how a species is able to utilize

human-altered habitats (in this case, a road) and how using such novel habitats introduces new variables into a complex foraging behavior. Investigating the off-road dropping behavior and discovering a connection between this drop and automobiles reveals more about gull ecology than studies which simply dismiss gulls as unintelligent, or dismiss sub-optimal behavior as a mistake not yet eliminated by natural selection. Comparative studies such as those comparing crows and gulls can be useful in identifying differences in behavior and prompting the investigation of the factors responsible for these differences. However, using comparison of skills as a direct measure of intelligence should be discouraged. Intelligence might be said to reflect how well-suited an animal is for its specific environment. Small, perhaps indistinguishable differences in environments may render a modification of the seemingly optimal behavior more appropriate in a given environment. Perhaps other prey-dropping birds do not require the off-road drop in their behavioral repertoire because they are not tame enough to be among humans, and therefore they do not drop onto any hard substrate frequented by vehicles. In contrast, evolution may already have acted upon the foraging behavior of the gulls, which often live in the presence of humans, to make the presence of automobiles an additional factor in the prey-dropping equation. Studying more closely the prey-dropping behavior of other birds, such as crows, that use roads may reveal that they, too, engage in the off-road drops occasionally.

## CHAPTER 2

While watching Herring Gulls forage on clams on Jamestown Island, James City County, Virginia, I occasionally observed the performance of a dropping behavior distinct from the typical foraging drop. Rather than dropping a clam onto the road, the gull would drop an object and then attempt to catch it before it landed. This behavior would then be repeated up to twelve times, in rapid succession.

My first hypothesis to explain this behavior is the Play Hypothesis, that the drop-catch is a form of play in gulls. Similar behavior has been labeled play in this and other bird species (Beck, 1982; Wheeler, 1943; Terry, 1990; King, 1970; Humphreys, 1964). However, as is typical of play studies, most of these reports are anecdotal and do not explain their rationale for classifying the behavior as play. In fact, the term “play” is often used as a largely untested default explanation when an observer forms the subjective opinion that a given behavior has no immediate function (Martin and Caro, 1985). In this study, I tested eight predictions of the Play Hypothesis which were based on a comprehensive review of play literature. In addition, I tested two alternative hypotheses to explain the dropping and catching of prey. The Kleptoparasite Detection Hypothesis is that foraging gulls use drop-catches in order to determine whether or not other gulls at the drop site are attentive and thus likely to attempt to steal the clams when dropped. The Repositioning Hypothesis is that the drop-catch is performed to reposition the clam in the gull’s beak in order to better orient the clam for a future drop onto a hard surface to break it open. The objective of this study was to test these three hypotheses for the function of an unusual behavior that has been casually observed and uncritically explained as play in the past (Warden, 1982; Sauer, 1978; Graham, 1988; Pandolfi, 1996; Negro et al., 1996). The predictions of these three hypotheses follow, and are summarized in Table 4.

## **Play Hypothesis**

### Bird Play

Because few animal species are known to play and the concept of animal play has been the subject of controversy, it is necessary to consider the documentation of play in birds before proposing that the drop-catch is play. The small group of animals reported to play is composed of both mammals and birds. Play has evolved mainly in K-selected species, or those with a prolonged period of immaturity, dependence on parental care, and high ratio of brain to body weight (Bekoff, 1984). In endotherms, families with higher total brain mass than expected by body size have more species that play than those with relatively smaller brains (Byers, 1999). Species with particularly high visual and manipulative capacities may also be particularly likely to play (Fagen, 1976; Pandolfi, 1996).

Some sources indicate that play in birds is rare, reportedly because their high body temperature, small size, and high activity lead to metabolic stress and low energy reserves (Barber, 1991; Morris, 1990). Another source suggests that evidence for play is strongest in birds (Gould and Gould, 1994). Sixteen out of 27 orders of birds contain primarily altricial species, and ten out of twelve orders of birds that do play contain altricial species, suggesting a relationship between degree of physical development at hatching and the presence of play. In addition, bird orders with more developed forebrains, such as the Psittaciformes (i.e. parrots) and the Passeriformes (i.e. songbirds), show more types of play (Ortega and Bekoff, 1987).

Corvids (i.e. crows and jays) possibly demonstrate the most complex play in birds. They drop and catch objects, engage in an activity which resembles a “king of the mountain” game, slide down snowy hills on their backs, and swing themselves around twigs or wires, holding on with one or both feet. One explanation for this amount of play in corvids is that they occupy a wide range of habitats (Lorenz, 1978). Play may help a bird learn about its specific surroundings, such as characteristics of local predators and



available prey items, allowing inhabitation of a wider range of environments (Ficken, 1977). Gulls also inhabit a wide range of habitats, suggesting that they, too, may have a use for play. Play has been reported in members of the avian order Charadriiformes, which includes gulls (Ortega and Bekoff, 1987). Herring Gulls were reported to land in a river above a water fall, float over the edge, and then fly back and repeat this behavior up to 21 times in a row (Knappen, 1930). A Pacific Gull (*Larus pacificus*) was seen dropping and catching a mussel while flying against a strong wind (Wheeler, 1943). Yearling Herring Gulls and yearling and juvenile Great Black-backed Gulls (*Larus marinus*) were also seen play-dropping objects, often catching the objects before they hit the ground (Beck, 1982).

Of the three categories into which play behavior is normally divided -- social, locomotor, and object -- birds most often engage in object play, or activity directed toward an inanimate object (Ortega and Bekoff, 1987; Ficken, 1977). This involves examining and testing objects found near the bird such as leaves, twigs, stones, or dead prey. The objects may be manipulated in any way, but may not be eaten even if they are edible (Morris, 1990; Pandolfi, 1996; Negro et al., 1996; Gould and Gould, 1994). Birds are thought to engage in large amounts of object play because they have highly developed visual skills and heavy reliance on vision (Ortega and Bekoff, 1987). To give some examples, Ascension Frigatebirds (*Fregata aquila*) catch feathers and seaweed from each other in the air while flying together, Inca Terns (*Lacosterna inca*) drop and retrieve objects while flying, and young Montagu's Harriers (*Circus pygargus*) and Peregrine Falcons (*Falco peregrinus*) pass vegetable fragments to each other in mid-air (Fagen, 1976; Pandolfi, 1996; Parker, 1975).

### Potential Costs of Play for Birds

Evidence for bird play is not necessarily evidence for Herring Gull play. Therefore, it will be useful to consider potential costs and benefits of play to Herring Gulls to evaluate the likelihood that they would engage in play behavior.

Play is thought to have several costs, the most obvious being the energy spent on the increased effort associated with play and the time spent in play that could be devoted to other beneficial activities (Bekoff and Byers, 1992). The drop-catch illustrates these costs in that more energy is put into performing the drop-catch than a normal foraging drop, due to the extra distance flown during the drops and catches. Also, the time spent drop-catching could instead be spent feeding or preening.

In fact, play typically consumes less than 10% of an animal's total daily time and energy expenditure. However, this seemingly small cost may not be representative of its importance. First, while some may consider this a minor cost, a study of pronghorn (*Antilocapra americana*) fawns demonstrated that using this small percentage of play energy towards growth could result in a 7% increase in fawn weight, enough to affect winter survival (Miller and Byers, 1991). Second, even activities requiring low time and energy, such as copulating, can have large benefits. Third, time and energy costs should be expressed as percentages of the time that the animal is active or of the energy left over after the fixed costs of resting metabolic rate (RMR) and growth are accounted for, rather than a percentage of the total time or energy budgets (Bekoff and Byers, 1992). The fawns mentioned previously used 2% of their total daily energy expenditure on play, but this equaled 20% of their daily energy expenditure beyond RMR and growth (Miller and Byers, 1991).

Another cost of play is lowered survivorship due to injuries or increased susceptibility to predation. For example, in one population of South American fur seals (*Arctocephalus australis*), 84.6% of the pups killed by sea lions were playing at the time of the attack, causing them to be distracted and farther from their mothers than non-playing young (Harcourt, 1991). Though predation on playing Herring Gulls was never actually observed during my study, the presence of eagles and hawks on Jamestown Island makes predation a potential cost for Herring Gulls. While these proposed costs of play seem reasonable, when all of these potential costs were explored in the play of cheetah (*Acinonyx jubatus*) cubs the overall cost of play was found to be low. Therefore, even if the benefits of play are minor, they might still outweigh the costs, preventing play from

being selected against (Caro, 1995).

### Potential Benefits of Play for Birds

Most studies suggest that play has adaptive consequences other than those expected of the behavioral systems to which the play is related, e.g. foraging (Barber, 1991). One idea is that play has a social function. By causing animals to interact, play allows young animals to become familiar and bond with fellow group members, compare their developmental competence with their peers, establish dominance hierarchies, and maintain sibling groups for ease of protection by parents (Vieira and Otta, 1998; Thompson, 1996). Challenges have been raised to each of these proposed social functions of play; for example, solitary species also play and play may peak before rank-associated encounters occur (Smith, 1982). Social functions seem unlikely as an explanation for the drop-catch since it may be performed by one gull without another present. A second idea regarding the function of play is that it allows the indirect practice of adult activities and the development of special skills, such as prey-capture maneuvers (Pandolfi, 1996; Negro et al., 1996; Pellis, 1981; Smith, 1982). This is especially useful when direct practice would be impractical or would expose the young animal to dangerous prey items or situations. Research on coyotes (*Canis latrans*) and kittens (*Felis domesticus*) has demonstrated a positive correlation between early playing and later prey-capture skills (Smith, 1982). A positive correlation was also demonstrated between amount of object play and rates of patting, biting, and grasping live prey in cheetah cubs (Caro, 1995). However, other studies have shown that animals can still hunt in a species-specific manner and do so successfully if deprived of play (Bekoff, 1976). Play in the form of a drop-catch could help juvenile gulls to forage more efficiently by allowing them to practice some component of the foraging drop, such as the steady release of the clam from the beak. A third idea is that play is used to develop behavioral flexibility, such that playing animals may not necessarily be practicing behavioral patterns that they will use regularly in adulthood but rather developing flexibility that will be helpful in making adjustments to novel situations.

This flexibility would be particularly useful to animals such as gulls that live in complex environments in which conditions change often, affecting habitat use and foraging (Fagen, 1984; Caro, 1995; Smith, 1982). Finally, a fourth idea is that play promotes physical training in young animals. This hypothesis posits that muscle groups which are used actively in adulthood might not develop properly without play. In addition to increasing muscular strength, play may improve aerobic capacity, endurance, and flexibility (Fagen, 1976; Fontaine, 1994). Physical training, too, is a possible function for a drop-catch performed in play, since flexibility is useful in a complex foraging technique such as prey-dropping. A challenge presented to this idea is that many effects of exercise can occur at any age and are short-lived, suggesting that general motor training is not the primary function of play. One study supporting this view indicated that only two of nineteen possible specific effects of elevated motor activity are permanent and available during a limited period of time: modification of cerebellar synaptogenesis and modification of skeletal muscle fiber type differentiation (Byers and Walker, 1995). Accepting one of these explanations does not necessarily mean that the others must be rejected. Play may have multiple functions (Thompson, 1996). In addition, different types of play may serve different functions (Fagen, 1976).

If play is beneficial, then selection could act to make play pleasurable, thus increasing the occurrence of a fitness-improving behavior within a lineage (Bekoff, 1976). Data indicate that increased levels of dopamine, endorphins, and norepinephrine are correlated with increased levels of play activity (Brownlee, 1997). Dopamine, which normally plays a role in reward, motivation, and motor patterning, does not appear specifically to target the neural circuitry responsible for play behavior but generally affects physical activity, non-selectively affecting play (Siviy et al., 1996). While the ultimate reason for playing may be for practice or physical training, the proximate reason may be that play is fun for an animal (Millar, 1981).

### The Drop-Catch as an Example of Play

The facts that birds have been reported to engage in play behavior many times and that some of the potential functions of play would benefit gulls lend credibility to the Play Hypothesis. However, this alone is not evidence enough that the drop-catch is play, since birds also engage in a variety of other behaviors that might relate to the drop-catch. Further, the potential functions of play are so broad that nearly any animal could be said to benefit from them; Herring Gulls are not unusual in this respect. This generality in the potential functions of play makes it easy to see how several play studies could quickly classify a behavior such as the drop-catch as play, without rigorous testing. Generality within the definition of play has also led to apparent intellectual laziness in the study of play and in the investigation of the drop-catch, specifically.

Just as the potential functions of play are so broad that they exclude few potential performers of play behavior, the definition of play is so broad that it excludes few behaviors. Play behavior takes so many different forms that any definition attempting to encompass all of the described examples of play is necessarily extremely general. One such definition is “apparently purposeless activity with no immediate adaptive goal, utilizing species-typical motor programs that are exaggerated in intensity or number of repetitions, or misordered compared to mature behavior, or mixed together with behavior appropriate to different contexts” (Gould and Gould, 1994: 164-165). Most of the elements of this definition are generally accepted as characterizing play, but the immediacy and the degree of benefits conferred by play are debated (Hall, 1998; Burghardt, 1998; Fagen, 1981; Bekoff and Byers, 1992; Martin and Caro, 1985). Some definitions state that play seems to have no purpose, while others state that play does not seem to serve the same purpose as the non-play behavior that it resembles (Pandolfi, 1996; Barber, 1991). This generality has made it easy for researchers to dismiss any enigmatic behavior as play without rigorous testing, tainting and cluttering this field of research. One example of such a behavior is the drop-catch, which is repetitive, utilizes motor programs typical of the Herring Gull feeding behavior, and seems to serve no immediate adaptive goal. General

definitions are useful in beginning to investigate a potential play behavior, but much more work must follow and, in many studies, does not.

Distinguishing play from other types of behavior might help to further define it. Play differs from typical adult behavior in that the behavioral elements which comprise play are repeated or misordered relative to the adult behavior or drawn from a variety of different adult contexts (Gould and Gould, 1994). Play fighting, for example, differs from mature adult fighting in that there is a different sequencing of behaviors. Also, behaviors from other contexts, such as copulation and feeding, are incorporated into the play fight (Pellis and Pellis, 1998). The drop-catch involves the repetition of the clam-release from the typical adult foraging drop, suggesting play. Another difference is that play involves the use of signals which are not used in other behavioral contexts. These signals elicit play and inhibit aggression in the animal receiving the behavior (Barber, 1991; Heinrich and Smolker, 1998). Many play signals are visual, such as the play face of primates, a loose-jawed grin. Other examples of visual play signals are the play bow of dogs, bears, and lions and the locomotor-rotational movements of Giant Pandas (*Ailuropoda melanoleuca*) and Pygmy Hippopotami (*Choeropsis liberiensis*) (Millar, 1981; Barber, 1991; Wilson and Kleiman, 1974). Play signals may also be auditory, chemical/olfactory, or tactile (Barber, 1991; Wilson and Kleiman, 1974). Perhaps part of the difficulty of identifying play in birds is due to the difficulty of recognizing any changes in their facial expressions which might signal play. They may use one of the other modalities of signaling, but no play signals in birds have yet been recognized. On the other hand, relaxed body tonus, which is often associated with play even though it is not considered a play signal (Pellis, 1981) is observed in Herring Gulls during the drop-catching behavior.

The next difference between play and mature behavior is that they are motivationally-distinct. Rather than trying to kill or injure each other, play fighting animals take certain measures to inhibit wounding. Larger or older animals may handicap themselves by adopting submissive positions or withdrawing their claws in order to prevent scratching (Pellis and Pellis, 1998). At the end of a play bout, no winner or loser has been established and there are no changes in dominance status or access to a resource

(Fagen, 1981). Similarly, in object play, the motivation is not to eat the object. By way of example, a tame grison (a small, carnivorous mammal of Central and South America) carried and flung around a mouse, stopped to eat a piece of another kind of meat, and then continued to play with the mouse, rather than simply killing and eating the mouse. Even though the grison was hungry while it was playing and the mouse was a potential prey item, it treated the mouse differently from its food object. That the grison's motivation in playing was not to eat was also suggested by the fact that it continued to play with the mouse after it had satisfied its hunger with the meat (Fagen, 1981). Similarly, if the drop-catch is play, the gulls should not eat the clam immediately after drop-catching.

Although play has been shown to be distinct from mature behavior, it must not be mistaken for immature behavior in which a young animal is simply making mistakes in attempting to perform adult behavior. Evidence for this is that adults play as well. In addition, play may emerge after the mature behavior upon which it is supposedly modeled has developed. For example, young coyotes fight to establish a dominance hierarchy and then begin to play fight once the hierarchy is stable (Barber, 1991). If the drop-catch is play it should be distinct from immature behavior in that adults should occasionally perform it and/or juvenile gulls should be capable of engaging in normal foraging behavior. A hypothetical example of immature behavior in gulls might be the off-road drop, which, according to the Experience Hypothesis (Chapter 1), young gulls perform simply because they have not yet learned to forage efficiently by targeting hard dropping substrates.

Finally, play is different from simple practice. The motivations are different, as demonstrated by play fighting. Play fighting is not used for fighting purposes but probably to form social bonds. Some characteristics of play fighting which cause it to be called play, such as the inhibition of wounding, are actually counterproductive to learning to fight well (Pellis and Pellis, 1998). In addition, unlike practice, play continues after mastery (Fagen, 1981). Therefore, if the drop-catch is play, it will be expected to continue even after juvenile gulls learn how to perform a foraging drop. Finally, variation increases with time in playful behavior, whereas variation decreases with time in non-play behavior as mastery is approached through practice (Fagen, 1981). A playing gull will be expected to increase

the variety in its drop-catch over time, perhaps in types of items dropped or number of repetitions over time.

### Predictions

Gulls are known to play and have reason to play, and the drop-catch fits a general definition of play behavior. Eight specific predictions of the Play Hypothesis (Table 4) are:

(1) *If the drop-catch is play, a higher proportion of the total drops performed by juveniles will be drop-catches than the proportion performed by older gulls.* Typically, young animals play more frequently than adult animals, possibly because altricial young do not have to devote time or energy to finding food or protecting themselves (Ortega and Bekoff, 1987; Hall, 1998; Bekoff, 1984). Precocial species, receiving little parental support, do, in fact, play less than altricial species. The order Charadriiformes, which contains the gulls, has an equal number of altricial and precocial species, suggesting that some but not all members of the order may play frequently (Ortega and Bekoff, 1987). By the previous argument, it would seem that adults do not play because they must spend time and energy feeding and protecting themselves. Another explanation is that adults maintain their physical condition by performing daily tasks so that play is not necessary except in times of low predation or high food availability (Fagen, 1976).

(2) *If the drop-catch is play, it will occur more often than the foraging drop over a soft substrate, such as water or grass.* Foraging birds aim specifically to break the shell, and therefore require a hard substrate below them, while playing birds would not be motivated to access the meat inside the shell, and therefore would not require a hard substrate. That foraging gulls target the road was demonstrated by the gulls on Jamestown Island, which dropped significantly more often over hard substrate than would be expected by chance given the small amount of hard substrate available (see Chapter 1).

(3) *If this is play, the drop-catch should be performed more, relative to foraging drops, when the number of gulls nearby increases.* This is based on the idea that the social environment must be conducive to play in order for it to occur. Object play is stimulated in



both kittens and Japanese monkeys (*Macaca fuscata*) by the mere presence of other individuals (Egan, 1976; Menzel, 1976). The effect of others may not be as dramatic in the gulls, since they are less social than kittens or monkeys. However, this difference in social structure may be less relevant with regard to the performance of object play than it would be to the performance of social play, which actually requires another individual. This is not a strong prediction, but based on a thorough review of the literature it appears that play is more likely in the presence of conspecifics.

*(4) If the drop-catch is play, a higher proportion of drop-catches, relative to foraging drops, will be performed in warmer temperatures than in colder temperatures.*

Environmental conditions must be appropriate for play to occur. In general, habitat type and resource availability can affect the amount and type of play (Bekoff, 1984). Poor weather will limit play, since an animal may need to conserve energy for thermoregulation. Food shortages also limit play, since a malnourished animal is less responsive to stimuli within its environment (Fagen, 1982; Bateson et al., 1990). Gulls on Jamestown Island would be expected to play less in extremely cold weather, in which they would need to devote energy to thermoregulation. The thermoneutral zone for birds, within which they do not need to devote extra energy to thermoregulation, is approximately 20-35 ° Celsius (Calder and King, 1974). Typically, the temperature on Jamestown Island between November and April is below this range, although a temperature of approximately 23 ° Celsius may be reached by April. Therefore, with increasing temperature, the proportion of drop-catches will be expected to increase consistently or, if the thermoneutral zone is reached, to increase and then level off.

*(5) The drop-catch, if play, will occur at higher average wind speeds than if it were foraging behavior.* Having a favorable environment for play would include having wind conditions that are conducive to flight (Bekoff, 1984). Although flight is energetically inexpensive in gulls relative to many other species, even their soaring flight requires the contraction of the pectoralis muscles to keep their wings steady (Pennycuick, 1975). In addition, while gulls have a metabolic rate of only twice their resting value when gliding,

they have a value of 6 -8 times their resting value when engaging in horizontal flapping flight, and even more energy is required for the ascending flapping flight required to get clams to a droppable height (Phillips et al., 1985: 25-27). Therefore, as wind speed increases and birds can rely more on gliding flight, they will have to expend less energy than they would in flapping flight. Confirming this idea, a study of the effects of wind on the field metabolic rates (FMR) of Northern Fulmars (*Fulmarus glacialis*), which have similar wing-loading and wing-shape to Herring Gulls, revealed that the FMRs were higher during lower wind speeds because the birds primarily use gliding flight while foraging (Furness and Bryant, 1996). This suggests that the drop-catch, if it is play, would more likely be performed during high winds, when flight is less costly. On the other hand, a bird performing a foraging drop, in which maximum control would be desirable, might drop during lower winds, in which accuracy would presumably be less compromised (Beck, 1982). This is not a strong prediction because the magnitude of the effect, or even if it would be detectable, is not known. However, available evidence suggests that higher wind speeds may promote drop-catches if they are play.

(6) *The object dropped, if the gull is drop-catching for play, will be a clam less often than in foraging drops.* Some studies suggest that play occurs most often with familiar objects in familiar environments (Fagen, 1976). Others, however, suggest that novelty in the environment stimulates play (Pellis, 1981; Wood-Gush and Vestergaard, 1991). If the drop-catch is play, it will be expected to occur often with clams but will also occur when a novel item is found, such as a piece of foil or flagging tape. While it might be rare for gulls to play with non-food items, since clams are readily available, gulls should never forage on non-food.

(7) *The object dropped in a drop-catch will not be eaten at the end of the drop series, unlike the object involved in a typical foraging drop.* This is based on the idea that the motivation for playing is different from the motivation for foraging and objects involved in object play are played with rather than eaten (Pellis and Pellis, 1998). Perhaps in a case where object play lasted for a significant amount of time, the animal's motivation could eventually change and the play object could ultimately be eaten. However, even the longest

series of drop-catches lasted substantially less than a minute, so it would seem that motivational state would be unlikely to change before the end of a series.

(8) *If play, the drop-catch series will not lead to the repositioning of the clam a greater-than-random proportion of the time (expected = 0.5).* This is because repositioning of the clam will be expected to be accidental rather than intentional; the clam will end up in its original position in the beak by the end of at least half of the series of drop-catches. It seems that the favorable position for carrying clams is with the hinge outward, allowing the thickest portion of the clam to be held between the tips of the mandibles and the thinner, tapered portion to point towards the throat. The shape of the beak may not accommodate the clam when held the other way, with the thickest portion of the clam pointing towards the throat. In this orientation, the gull may have less control over the clam and could drop it or gag on it. Therefore, the Play Hypothesis predicts that the clam will not be repositioned more than expected by chance, and it may be repositioned less than expected by chance if there is a highly favored position for the clam.

### **Kleptoparasite Detection Hypothesis**

Kleptoparasitism, occasionally called piracy, robbery, pilfering, or food parasitism, is when one individual steals the food that another, the host, has obtained (Brockmann and Barnard, 1979). The Kleptoparasite Detection Hypothesis is that the drop-catch allows a gull to determine if other gulls in the area are attentive and likely to attempt to steal its clam. A gull could test the likelihood of theft before actually relinquishing control of a clam by dropping the clam as if it were going to allow the clam to hit the ground and then catching it. If other gulls at the drop site flew towards the host gull or moved towards the spot where the test-dropped clam would have landed, the host could select a different drop site.

### **Ecological Conditions Favoring Kleptoparasitism**

Several ecological conditions facilitate the evolution of kleptoparasitism. First is the

transportation of large quantities of food. A second is the transportation of particularly large or high-quality food items, such as energy-rich prey items like clams. A third is predictable feeding habits of the host, such as a parent that regularly returns to a nest with food. The feeding habits of the Herring Gulls on Jamestown Island are predictable since, after acquiring a clam, the birds have the choice of only the rocky island or the road on which to drop the clam. A fourth ecological condition that might lead to the evolution of kleptoparasitism is the conspicuous carrying of food (Brockmann and Barnard, 1979). For example, piracy on bald eagles (*Haliaeetus leucocephalus*) usually occurred when one eagle saw another carrying or eating a fish (Fischer, 1985). A distant observer, and therefore, presumably, another gull, can easily see whether or not a gull is carrying a clam. Thus, the ecological conditions of the gulls on Jamestown Island favor the development of kleptoparasitism, indicating the potential need for an anti-kleptoparasitism mechanism.

#### Species Characteristics Favoring Kleptoparasitism

Members of the order Charadriiformes, including the gulls, exhibit many ecological and behavioral traits which facilitate the evolution of kleptoparasitism in animals. Many kleptoparasitic species are opportunists, feeding on a variety of items whenever they become available. Many also demonstrate particular aerial agility, in the case of kleptoparasitic bird species. In fact, many Charadriiformes, particularly of the gull family (*Laridae*), have been observed kleptoparasitizing other birds. Some gulls obtain a large proportion of their diet through stealing (Brockmann and Barnard, 1979). Juvenile Herring Gulls, specifically, are less efficient at procuring food themselves and therefore resort more frequently to kleptoparasitism (Verbeek, 1977c). Thus, kleptoparasitism is likely to occur among the Herring Gulls on Jamestown Island, indicating that putative anti-kleptoparasitism measures such as the drop-catch could be necessary.

### Potential Need for Anti-Parasitism Mechanisms

Several anti-kleptoparasitism methods have been described in Bald Eagles, but these do not include anything resembling the drop-catch. Nine anti-kleptoparasitism behaviors observed in Bald Eagles were: feeding away from others, feeding when few others are present, selecting small prey items, concealing prey, continuing to act as if searching for prey after finding prey, choosing protected eating sites, using aerial maneuvers to elude kleptoparasites, using threat displays, and spreading their wings over prey items to conceal them (Fischer, 1985). Herring Gulls, too, employ some of these methods, such as feeding away from others when several gulls are at the drop site (personal observation). This suggests a high risk of theft in this population and a need for additional anti-kleptoparasitism mechanisms. Because the ecological conditions and species characteristics of the Herring Gulls at Jamestown Island favor kleptoparasitism, an anti-kleptoparasitism mechanism would seem to be adaptive.

### Predictions

Herring Gulls on Jamestown Island are subject to and required to defend themselves against kleptoparasitism, and the drop-catch may serve this purpose. Eight specific predictions of the Kleptoparasite Detection Hypothesis (Table 4) are:

(1) *If the drop-catch behavior is used for kleptoparasitism assessment, a lower proportion of young than adults will perform it.* A study on Kelp Gulls showed that juveniles engaged in more kleptoparasitic attacks even though all age classes were equally successful in retaining and stealing prey (Steele and Hockey, 1995). This seems to be true of the Herring Gulls on Jamestown Island as well (unpublished data, D. Cristol). Adult Herring Gulls will be more subject to kleptoparasitism pressure than young gulls and it therefore would be adaptive for them to perform the drop-catch more often in order to defend their prey items.

(2) *The drop-catch will occur, on average, over the same hard substrate as the foraging*

*drop*. Presumably, the gull will be doing the test drop over an area onto which it actually intends to drop the clam.

(3) *If used in kleptoparasitism risk assessment, the drop-catch will occur a greater proportion of the time, relative to foraging drops, when more potentially-kleptoparasitic gulls are around the drop site.* Kleptoparasitism is most likely to evolve in ecological conditions where there is a large number of hosts. Food-stealing occurs most often among colonial seabirds which are packed together on small islands for nesting (Brockmann and Barnard, 1979). Although the Herring Gulls on Jamestown Island are not nesting, they are often crowded onto the limited sections of hard-substrate available at the site, perhaps waiting to parasitize incoming gulls (personal observation). This is the critical prediction of the Kleptoparasite Detection Hypothesis.

(4) *If drop-catches are being used for kleptoparasitism assessment, the drop-catch will be performed more often in low temperatures, as is the case in foraging, since both are used to gain energy through eating.* A food shortage occurring during a particular year or season or a period of poor weather in which efficient foraging is more difficult will prompt kleptoparasitism to occur (Brockmann and Barnard, 1979). Extremely cold weather can be viewed as effectively creating a food shortage; the same number of clams will be present, but gulls will need extra energy for thermoregulation and thus theft will be more costly. With increasing temperature, the proportion of drop-catches will be expected to decrease consistently or, if temperatures reach the gulls' thermoneutral zone, decrease and then level off.

(5) *A greater proportion of drop-catches will be observed at lower average wind speeds.* As with low temperatures, clams will become more valuable at low wind speeds because the energy spent in flight will be greater and thus the motivation to avoid being kleptoparasitized will be greater. Supporting this prediction is the fact that kleptoparasitism in kestrels increased when the wind was weak, making it unfavorable for flight-hunting (Fritz, 1998). Though kestrels and gulls have different styles of flight, gulls also use less energy in flight during periods of high wind (Phillips et al., 1985: 25-27) and therefore might be expected to kleptoparasitize other birds more in low winds. This is not a strong

prediction because it is not known whether the magnitude of a putative wind effect would be detectable.

(6) *The object dropped will always be a clam, since the motivation is to eat the dropped object after testing for the presence of kleptoparasites.*

(7) *The dropped object will be eaten at the end of a drop series involving a drop-catch as often as at the end of a drop series involving only normal foraging drops. The purpose of the drop-catch is to protect the clam from other gulls in order to eat it. The motivation for drop-catching is the same as for foraging, namely, hunger.*

(8) *Finally, as also predicted by the Play Hypothesis, the gulls will not reposition the clams in their beaks by the end of more than half of the drop-catch series. The clam will be randomly reoriented by the end of a given series of drop-catches or will be returned to the same favored position in the beak.*

### **Repositioning Hypothesis**

The Repositioning Hypothesis is that gulls perform the drop-catch in order to reposition the clams in their beaks for a more efficient drop. This assumes that, on occasion, gulls extract clams from the mud and begin flying before orienting them appropriately in the beak, or lose their grip while flying and must re-orient the clams. Because repositioning behavior in prey-dropping birds has never before been studied, only three predictions supporting the Repositioning Hypothesis (Table 4) can be confidently proposed:

(1) *The object involved in the drop-catch will always be a clam, since other prey items of the Herring Gulls on Jamestown Island do not need to be dropped, let alone reoriented.*

(2) *The clam will be eaten at the end of a drop series involving a drop-catch as often as at the end of a drop series only involving normal foraging drops. The purpose of the drop-catch is to orient the clam in a way that will cause it to open more easily when it is*

dropped, allowing the gull to eat it. Hunger is the motivation for the drop-catch, as it is for foraging.

*(3) Finally, the critical prediction is that the clam will be repositioned in the gull's beak by the end of a series of drop-catches a greater-than-expected (by chance) proportion of the time if this drop-catch is performed for the purpose of repositioning the clam for dropping.*

## METHODS AND RESULTS

### Methods

In order to determine the function of a drop-catch behavior distinct from the typical foraging drop of the Herring Gull, I observed gulls feeding and resting on the mud flats at Sandy Bay, east of the isthmus road to Jamestown Island. Herring Gull behavior was observed for approximately 80 h on 38 days for 1-3 h surrounding low tide periods from November to April 1997/98, 1998/99, and 1999/2000.

With a few exceptions, the same variables were measured in this study as in the off-road drop study described in Chapter 1. In this case, the object dropped was not always a clam, so object identity (clam, stick, fish, shell, or other) was recorded for each drop. The substrate over which the object was dropped was not limited to grass and road in this study; substrate type recorded for each drop also included water, mud, and island (a rocky 3-m X 8-m island was located approximately 140 m east of the isthmus road). In addition, any repositioning of the clam in the beak following a drop-catch was noted. Furthermore, air temperature was recorded using the Ultimeter 100 weather station in order to determine the relationship between drop-catches and this environmental variable. These values were later lumped into 5<sup>o</sup>-Celsius categories which provided approximately equal sample sizes for each category of temperature. Gulls within 5 m of the drop site were recorded as other gulls present at drop site. An exception was made for birds dropping on the island, where gulls within 2 m of the drop site were recorded as other gulls present. This difference was

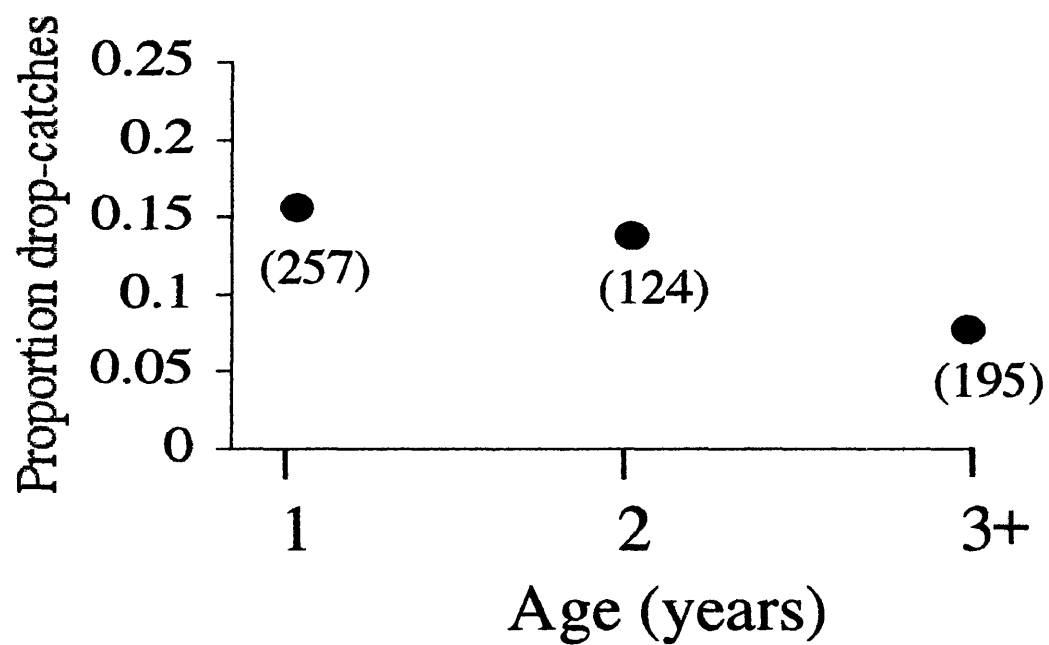


due to the fact that space was limited on the island so gulls using the island for preening, rather than interfering with a drop, could coincidentally be within 5 m of the clam-dropping gull. In contrast, so much of the road was available that a gull could use a patch without being near another gull -- if another gull was observed within a 5-m radius of the clam-dropping gull, it was likely to be attempting to interfere with the drop. Unlike the previous study the presence of cars was not recorded in this study.

Results are presented as number of drop-catches divided by number of typical foraging drops seen under the same circumstances. Groups were compared using Chi-square tests. Only the first drop in a series of foraging drops performed with the same clam was used in the analysis, to avoid pseudoreplication. The drop-catch occurred so infrequently that I used the first drop-catch in a series, whether it was the first drop or not. Repositioning was recorded as a change in orientation from before the first drop-catch to after the last drop-catch in a series.

## Results

I began analysis by comparing the proportion of drop-catches, relative to foraging drops, for each age. As predicted by the Play Hypothesis and contrary to the Kleptoparasite Detection Hypothesis, a negative relationship with age was observed and the differences in relative proportions of drop-catches by age were significant ( $X^2 = 6.4$ ,  $df = 2$ ,  $p = 0.039$ ; Fig. 5). (Due to the low sample size for fourth-year gulls, drops for third- and fourth-year birds were combined.) I then compared the proportion of drop-catches, relative to foraging drops, for soft versus hard substrate. As predicted by the Play Hypothesis and contrary to the Kleptoparasite Detection Hypothesis, drop-catches were more frequent than foraging drops over soft substrate ( $X^2 = 94.8$ ,  $df = 1$ ,  $p < 0.0001$ ). I compared the proportion of drop-catches, relative to foraging drops, during the presence of 0, 1, 2, 3, and >4 other gulls. Contrary to a prediction of the Play Hypothesis and the critical prediction of the Kleptoparasite Detection Hypothesis, a negative relationship with number of other gulls present was observed, with the difference in relative proportions for



**Figure 5.** Relationship of drop-catches and age of gulls. Parentheses indicate sample sizes.

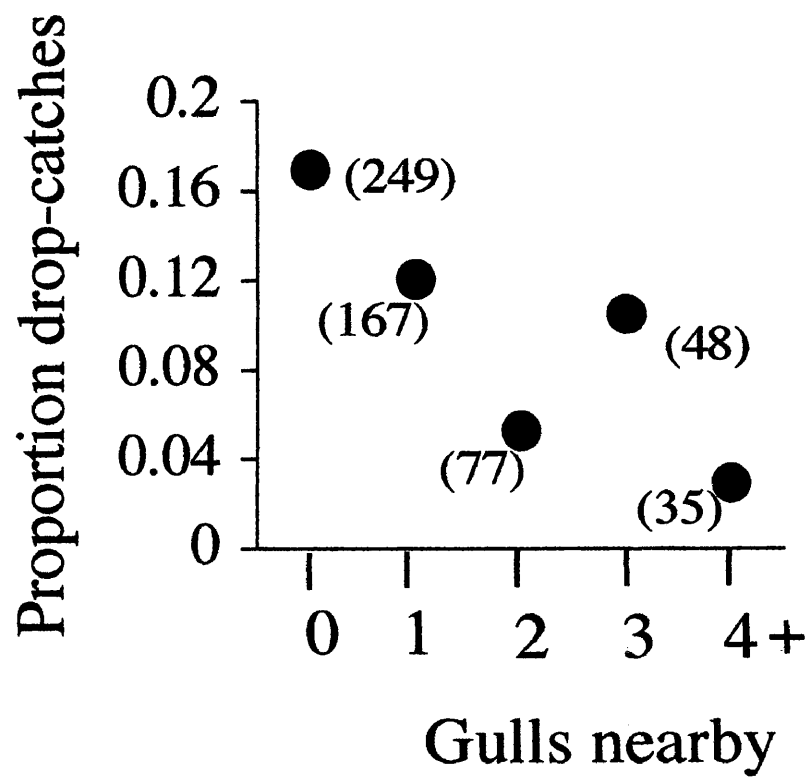
each category being significant ( $X^2 = 11.3$ ,  $df = 4$ ,  $p = 0.023$ ; Fig. 6). In other words, although the result was significant, it was in the opposite direction of that predicted by any hypothesis. The proportion of drop-catches, relative to foraging drops, for each 5 °Celsius temperature interval were then compared. As predicted by the Play but not the Kleptoparasite Detection Hypothesis, a positive relationship with temperature was observed, and the difference in relative proportions of the temperature categories was significant ( $X^2 = 19.6$ ,  $df = 6$ ,  $p = 0.003$ ; Fig. 7). A post hoc comparison revealed a significant difference between the proportion of drop-catches, relative to foraging drops, during the warmest and coldest temperature intervals ( $X^2 = 10.7$ ,  $df = 1$ ,  $p = 0.001$ ).

Next, I compared the proportion of drop-catches, relative to foraging drops, for each five-km/h wind interval. As predicted by the Play Hypothesis but not the Kleptoparasite Detection Hypothesis, a positive relationship with wind speed was observed, and the differences in relative proportions by wind speed were significant ( $X^2 = 29.0$ ,  $df = 4$ ,  $p < 0.0001$ ; Fig. 8). A post hoc comparison revealed a significant difference between the proportion of drop-catches, relative to foraging drops, performed during the highest and lowest wind speed intervals ( $X^2 = 15.1$ ,  $df = 1$ ,  $p < 0.0001$ ).

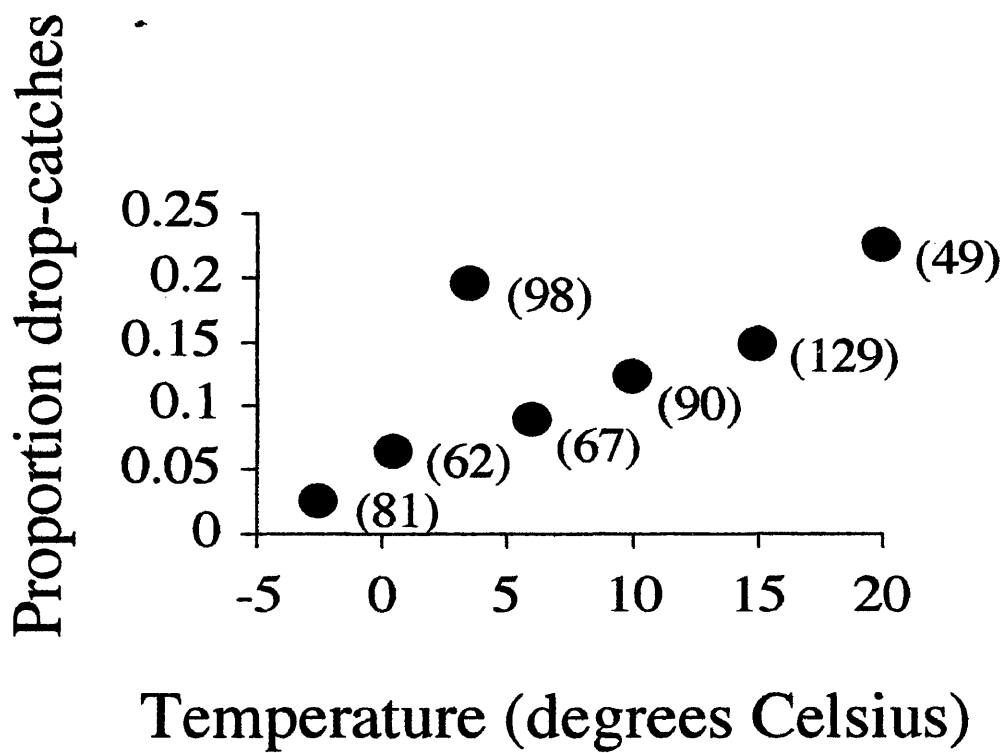
Sixth, in accordance with the Play Hypothesis but not the other two hypotheses, I found that drops performed with clams were drop-catches significantly less often (0.0941,  $n = 542$ ), relative to foraging drops, than drops performed with non-clams (0.6176,  $n = 34$ ) ( $X^2 = 80.2$ ,  $df = 1$ ,  $p < 0.0001$ ).

Seventh, also in accordance with the Play Hypothesis and not the other two, I found that clams that were eaten at the end of a drop series had been involved in drop-catches significantly less often (0.0034,  $n = 297$ ) than clams that were not eaten at the end of a drop series (0.1938,  $n = 258$ ) ( $X^2 = 49.7$ ,  $df = 1$ ,  $p < 0.0001$ ).

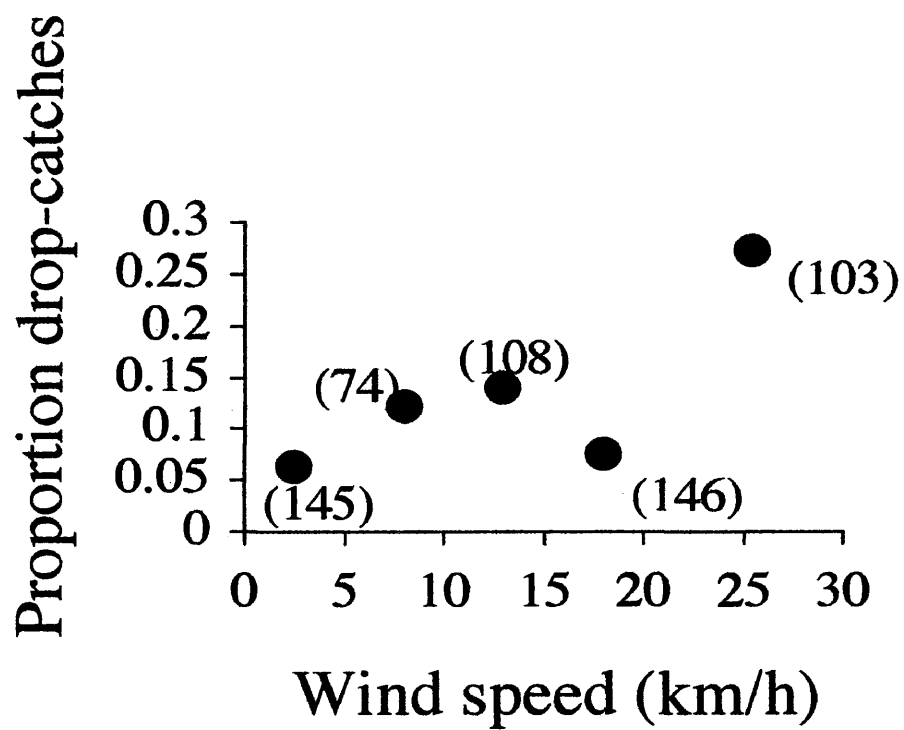
Finally, contrary to the critical prediction of the Repositioning Hypothesis, I found that the clam was returned to its original orientation by the end of nine out of thirteen drop-catch series and was reoriented by the end of only four out of thirteen drop-catch series.



**Figure 6.** Relationship of drop-catches and presence of other gulls. Parentheses indicate sample sizes.



**Figure 7.** Relationship of drop-catches and temperature. Parentheses indicate sample sizes.



**Figure 8.** Relationship of drop-catches and wind speed.  
Parentheses indicate sample sizes.

**Table 4. Summary of drop-catch predictions and results.**

	<u>Kleptoparasite Detection Hypothesis <sup>a</sup></u>	<u>Repositioning Hypothesis <sup>a</sup></u>	<u>Play Hypothesis <sup>a</sup></u>	<u>Observed Relationship <sup>b</sup></u>
<b>Age</b> (1 --> 4+ yrs)	+		=	=
<b>Substrate</b> (soft --> hard)	+		=	=
<b># of Others Present</b> (0 --> 4+)	+		+	(=)
<b>Temperature</b> (-5 --> 25° Celsius)	=		+	+
<b>Wind Speed</b> (0 --> 30 km/h)	=		+	+
<b>Object</b> (clam, other)	=	=	+	+
<b>Clam Fate</b> (eaten, not)	=	=	+	+
<b>Repositioned</b> (no, yes)	=	+	=	(=)

<sup>a</sup> Predicted relationships (slopes) of variables putatively affecting occurrence of drop-catches for the Kleptoparasite Detection, Repositioning, and Play Hypotheses; <sup>b</sup> X<sup>2</sup> test revealed significant difference in proportions of drop-catches at different levels of this variable except for those in parentheses.

## DISCUSSION

While play in mammals has been thoroughly studied, play in birds has not been well documented and has been said to be rare or absent (Barber, 1991; Morris, 1990). Much of the evidence for play in birds is either strictly related to corvids (i.e., crows and jays) or is anecdotal (Lorenz, 1978; Graham, 1988; Sauer, 1978; Terry, 1990; Warden, 1982). Beck (1982) conducted a study in which, measuring some of the same variables as those in this study (e.g., wind and substrate), he concluded that the drop-catch behavior performed by Herring Gulls was play. However, he did not observe this behavior in immature Herring Gulls other than yearlings. Also, as in many studies of play, he did not provide and test alternative explanations to the hypothesis that the drop-catch behavior is play (Beck, 1982). My study tested multiple predictions of a Play Hypothesis based on play research from birds and mammals, as well as the predictions of two alternative hypotheses, the Repositioning Hypothesis and the Kleptoparasite Detection Hypothesis. I conclude that the Play Hypothesis should not be rejected as an explanation for the drop-catch behavior.

Characteristics of the drop-catch behavior itself, the gulls performing it, and the environmental conditions surrounding it are all suggestive of play behavior. Seven of eight predictions associated with the Play Hypothesis were supported by observations of the Herring Gulls on Jamestown Island, while one of eight predictions of the Kleptoparasite Detection Hypothesis, and zero of three predictions of the Repositioning Hypothesis, were met.

Consistent with the Play Hypothesis, younger gulls performed more of the drop-catch behavior than older gulls. In addition, the drop-catch was performed over soft substrate significantly more often than foraging drops, suggesting that drop-catches were distinct from foraging behavior and not related to food acquisition. Increasing wind speeds and increasing temperatures increased the chance that a drop-catch would occur, which was predicted by the Play Hypothesis since play occurs in favorable conditions, in this case, favorable for devoting less energy to flight and thermoregulation. The drop-catch was



performed with a non-clam significantly more often than other types of drops and the clam was eaten significantly less often at the end of a drop series involving a drop-catch than at the end of a series not involving a drop-catch, both suggesting that drop-catch behavior is distinct from foraging.

One prediction made by the Play Hypothesis that was not met was that the frequency of the drop-catch behavior would increase as the number of other gulls present at the drop site increased. Even though object play may be performed solitarily, I suspected that the presence of other gulls at the drop site would increase the incidence of play since, at least in kittens and monkeys, the presence of others encourages animals to play with objects (Egan, 1976; Menzel, 1976). However, perhaps the sociality of kittens and monkeys influences this effect on play, while other gulls are simply viewed as potential thieves of the play object. This finding does allow firm rejection of the Kleptoparasite Detection Hypothesis, since increasing the number of potential parasites nearby should necessarily increase the threat of kleptoparasitism.

A behavior distinct from the drop-catch was recognized during the observation period which more convincingly appears to serve an anti-kleptoparasitism function. Arriving at crowded drop sites, gulls often would either turn away and fly to different drop sites or hover as if preparing to drop the clam and then descend to the ground while still holding the clam. Occasionally, gulls would ascend and descend several times while maintaining their hold on the clams before actually dropping the clams at the site or choosing different sites. Gulls also appeared to slightly reposition clams by means other than the drop-catch. Several gulls were seen lowering their heads while flying and loosening their grip on, rather than completely releasing, the clams. This led to slight adjustments in the position of the clams in the beak rather than total reorientation and allowed the gulls more control over the clams than would drop-catches.

While the immediate function of the drop-catch, as play, should be to provide pleasure to the gull, there are several potential long-term benefits. The drop-catch may function to allow young gulls to improve the foraging drop used in opening clams. Supporting the idea that play functions to allow a young animal to practice mature behavior,

this improvement could be achieved through their practicing a specific skill (Negro et al., 1996), such as releasing the clam a certain way or aiming at some spot below. Instead, the drop-catch may allow a gull to practice the recovery of a clam dropped accidentally by itself or another gull. Rather than serving a practice function, the drop-catch behavior might help young gulls to improve their foraging drop by generally training muscles or establishing neural connections, which could give them greater strength or agility later (Fontaine, 1994). Alternatively, the drop-catch might encourage exploration, allowing young gulls to learn about potential prey items in their specific environment (Ficken, 1977). The observation that non-clams were dropped is consistent with this idea. The drop-catch may serve more than one of these functions (Thompson, 1996). I have rejected two alternatives to the idea that this behavior is play, and found results largely consistent with the idea that drop-catch behavior in Herring Gulls is a form of object play. Until other alternative hypotheses are proposed, I conclude that this behavior is play.

## GENERAL DISCUSSION

Simple optimality theory asserts that an animal will perform the behavioral alternative that leads to the greatest net energy gain. However, constraints such as competition and predation may prevent an animal from doing so. In addition, optimality may be measured in currencies other than net energy gain. The purpose of using optimality theory to investigate a behavior is simply to better understand the forces influencing an animal which lead to its performance of a particular behavioral alternative.

A model of optimal foraging for avian prey-dropping predicts that the Herring Gulls on Jamestown Island should drop their clams over the hardest substrate available, i.e., the road (Switzer and Cristol, 1999). However, the gulls were occasionally observed dropping onto the grass along the road instead. The prediction that gulls should drop onto the hardest available substrate is also violated by the drop-catch behavior I observed, in which the clam was caught before it hit the ground. The drop-catch behavior violates a second prediction of optimal foraging as well, that the gulls should minimize the height to which they fly when dropping prey (Cristol and Switzer, 1999). By dropping and catching clams, gulls are adding to the total height flown without subjecting clams to additional striking of the substrate. In other words, they are wasting energy.

In my study of off-road drops, Herring Gulls did not appear to be maximizing net energy gain by dropping clams onto the grass. Thus, I proposed several hypotheses to explain the sub-optimal behavior. I found a previously-unrecognized constraint affecting Herring Gulls that use the roads as foraging substrates, namely the presence of automobiles. The birds appear to drop clams as the cars approach, perhaps in a fear response to the approach of a potential predator. This result was surprising considering that I had observed vehicles having to stop on the road leading out to Jamestown Island while waiting for Herring Gulls to finish tiny remaining pieces of clam in the center of the road. Often, gulls would walk rather than fly to the side of the road after finishing (personal observation). Also, Herring Gulls are abundant and widely-distributed among human populations, feeding on waste from dumps and fisheries and inhabiting man-made areas such as parking lots and runways (Pierotti and Good, 1994). Therefore, their fear of

areas such as parking lots and runways (Pierotti and Good, 1994). Therefore, their fear of or distraction by human activity would not seem to be great enough to merit wasting an energetically valuable clam to escape from a slow-moving vehicle. However, three other hypotheses were firmly rejected: (1) strong wind blowing the clams onto the grass; (2) clams opening without breaking on grassy substrate; and (3) the presence of other gulls on the road leading less competitive individuals to use a sub-optimal but less crowded drop site. There was a non-significant trend supporting a fourth hypothesis, the inexperience of juvenile gulls; age may influence a gull's response to automobiles.

In my study of drop-catch behavior, simple optimality theory generally suggested that net energy gain was not the currency being maximized by this behavior and that acquiring food was not the main motivation behind it. All but one of the predictions of the hypothesis that the drop-catch is play, rather than foraging behavior, were supported by the data collected from 576 drops. The two alternative hypotheses, that drop-catches serve to reveal risk of theft or to reposition clams for more accurate dropping, were clearly rejected by the same data.

Some people unfamiliar with optimality theory believe that if an animal is shown to behave in an energetically inefficient manner, optimality theory is proven incorrect. These two studies revealed that variations on the typical foraging drop, off-road drops or drop-catches, did not lead to a maximum net energy gain. Instead of rejecting the idea that evolution has shaped animals to behave efficiently, I conclude that my studies have revealed two constraints on gull foraging not usually included in optimal foraging models. One is that the presence of automobiles may disrupt these animals which are otherwise highly adapted for life among humans. The other is that young gulls play in a manner that directly conflicts with foraging efficiently. Both studies demonstrate that optimality theory provides a useful framework for understanding the constraints on behavior.

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