

Why does parental effort of the common tern (*Sterna hirundo*) decrease after a late-season flooding event? A multi-hypothesis approach

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Abstract:

The production of two clutches within the same breeding season is uncommon amongst many shorebirds species, and even more rare is the act of double-brooding. In late June of 2006, heavy rains flooded over 120 common tern (*Sterna hirundo*) nests, causing a re-nesting effort of over 140 pairs, and perhaps one case of double-brooding. To evaluate the level of parental effort after a late-season flooding event, I weighed and then compared the eggs of the second clutches to corresponding egg data from the first clutches of 1983 and 1984 from the same colony on Oneida Lake, NY. The mean egg weights from the second clutch of 2006 all weighed significantly less than the corresponding mean egg weights of the first clutches of 1983 and 1984. In both first and second clutches, there was a linear decrease in egg weight with laying order. Three hypotheses have been postulated to explain the intraclutch variation of egg weights, the “brood-survival”, “brood-reduction”, and “insurance” hypotheses. Given the circumstances of 2006, the brood-reduction hypothesis fits best at explaining the intraclutch variation in egg weights.

The observed decline in parental effort late in the season can be explained by the “timing” hypothesis, which in the case of this study included a decreased food supply and reduced breeding synchrony later in the season. Certain aspects of the life history of common terns such as molt, which overlapped with the production of the second clutch, as well as the allocation of energy between parents in a bi-parental care system, also decreased the success of many second clutches. Many adults associated with second clutch nests abandoned their eggs and/or chicks in order to enhance the probability of their own survival.

Introduction:

During the summer of 2006, a large storm on June 28th produced high waters on Oneida Lake, New York, that flooded approximately 30% of the surface area of Little Island, the island on which a colony of common terns (*Sterna hirundo*) breed. Shortly following this flood, many pairs re-nested, thereby producing a second clutch. This study therefore presented itself as an opportunistic chance to observe the recovery effort of a tern colony after a late-season flooding event. As compared to previous studies, this study is unique in that it studies the effects of a stochastic environmental event, instead of an experimental manipulation, on the fate of a second clutch.

I hypothesized that the second clutch eggs of 2006 will weigh less than the first clutch eggs of 1983 and 1984, in effect showing a decreased parental effort. 1983 and

1984 were chosen as the “control” years with which to compare the 2006 data because a study conducted by Bollinger (1988) on the same colony of Oneida Lake included first clutch egg weights during seasons when the colony did not experience any large-scale perturbations such as the flood during 2006. The fact that the tern colony on Oneida Lake has maintained a stable population since 1983 is imperative to this study. In order to understand the level of parental effort terns invest in reproduction, it is necessary to examine the current hypotheses regarding various dimensions of reproductive strategy.

Egg production is a characteristic common to all birds, but the diversity of egg-laying strategies is nearly as diverse as the birds that lay them. For instance, snow geese (*Chen caerulescens*) are determinate breeders that rely on nutrient reserves for egg-laying, and thus they produce a predictable clutch of three eggs per season (Ankney and MacInnes 1978). On the other hand, many species of passerines are income breeders that acquire food and nutrients at the breeding grounds on a daily basis, which allows these species to lay eggs indeterminately; the common tern (*Sterna hirundo*) is also an income breeder.

An intraclutch variation amongst egg weights has also been shown for many species. Howe (1978) showed that common grackles (*Quiscalus quiscula*) increase the provisioning of yolk and albumen with the order of laying, so the last egg laid is the heaviest. Conversely, many waterbird species such as gulls show a decrease in egg weight with clutch order, the last egg weighing the least (Parsons, 1976). Table 1, taken from Slagsvold et al. (1984), represents a brief survey of clutch characteristics of both passerines and non-passerines, and the values of “Relative size of last egg” reflect a range

of avian intraclutch egg variation. Notably, birds with a relatively small last egg typically lay larger eggs, while birds with a relatively large last egg lay eggs of a smaller volume.

Three hypotheses have been formed concerning avian intraclutch variation: the “brood-reduction hypothesis”, the “brood-survival hypothesis”, and the “insurance hypothesis”. According to Lack’s brood-reduction hypothesis (1954), last-hatched chicks are smaller due to hatching asynchrony, thus facilitating starvation of the youngest sibling when food resources are low. This is deemed adaptive because loss of one chick could prevent starvation of the entire brood. On the other hand, many passerines adopt the brood-survival hypothesis, where the last laid egg weighs the heaviest to increase the likelihood of survival for the last-hatched chick due to hatching asynchrony. In the insurance hypothesis (Dorward, 1962), it follows that the last-hatched sibling serves as “insurance” in case an older sibling is lost. Table 2 shows two opposing aspects of life-history, altricial vs. precociality, as well as two features of ecology, hole-nesting vs. open-nesting, and how these four factors can affect the trend of intraclutch variation in both passerines and non-passerines. The patterns shown Table 2 can be explained with the previously mentioned hypotheses. Altricial non-passerines have a relatively small last egg, which most likely fits the insurance hypothesis because their nests are exposed and the chicks may be highly vulnerable. If an older chick were lost due to predation or starvation, the last-hatched chick could serve as insurance and replace the lost chick. However, the last laid egg of cavity-dwelling passerines is nearly the same size as the previous eggs of the clutch, suggesting in this group, where the eggs are more protected, that the brood survival hypothesis applies because each egg might be expected to have the same probability of survival. Bollinger (1988) concluded that the brood reduction

hypothesis did not explain the intraclutch decline in egg weights, rather the insurance hypothesis seemed to fit best. These three hypotheses not only offer an explanation to the intraclutch variation among egg weights, but also help account for the fate of the clutch post-hatching.

A seasonal decline in reproductive success is typical for birds with rigidly defined breeding seasons (Perrins, 1996). Two hypotheses have been formed concerning this seasonal decline: the “timing” hypothesis and the “parental quality” hypothesis. Under the timing hypothesis, reproductive success declines with a later lay date because of factors such as reduced breeding synchrony of the colony and changing environmental conditions later in the season, such as a decreasing food supply (Arnold et al., 2004). On the other hand, the parental quality hypothesis states that reproductive success declines later in the season because birds that lay later in the season are typically younger, are less experienced, and are of lower quality (i.e. cannot obtain a high-quality territory for breeding) than the birds that lay earlier in the season (Hatchwell, 1991). My study seems to give support only to the timing hypotheses. The timing hypothesis is supported because the number of yellow perch (*Perca flavescens*) under 4”, a regular part of the tern diet, decreased nearly 40-fold from early June until early August, and breeding synchrony of the colony greatly decreased as the season progressed as well. Not enough data were collected to assess any measure of parental quality that might either support or refute the parental quality hypothesis.

Terns have historically been considered a sub-family, Sterninae, of the gull family Laridae, however, new molecular evidence suggests that terns comprise an entire family unto themselves, Sternidae (Sibley and Ahlquist 1990; Chu 1997). Although molecular

evidence shows this split and suggests elevation of the group to the family level, the life history and ecology of individuals within these two families are still very similar. For instance, two life-history traits that many gulls and terns share are migration and colonial nesting.

Common terns are neotropical migrants that usually produce one clutch of three eggs per season (Arnold et al. 2004). However, the production of second clutches in terns has been examined and reported in many studies (Massey and Atwood 1981; Wiggins et al. 1984; Moore and Morris 2005). In addition, several studies have addressed the possible rearing of two broods within the same season in species such as the little penguin (Johannesen et al. 2003), the great tit (Verboven and Verhulst 1996), and the common tern (Moore and Morris 2005). Moreover, Yuan (1993) reported seven possible instances of double-brooding on Oneida Lake in 1988 and '89. Two wide-ranging conditions have been correlated with the production of two broods within a season: an unusually large food supply, and the appearance of early breeding pairs in earlier than normal breeding seasons (Moore and Morris 2005). Many tern species such as the sooty tern (*S. fuscata*, Harrington 1974) and the Arctic tern (*S. paradisaea*, Coulson and Horobin 1976) have been reported to show a pattern of an early return by older, more experienced birds. Moore and Morris (2005) believe that the dearth of double-brooding in terns is due to their life history. They argue that a species whose chicks grow slowly with a relatively long developmental period, and whose parents have a compressed breeding season have very little chance at successfully rearing two broods in one season. This is because rearing two broods in the same season is physiologically taxing on a bird, particularly for long-distance migrants.

Lack (1947) hypothesized that clutch size is variable amongst individuals, and therefore can be acted upon by natural selection. His hypothesis, now simply known as Lack's Hypothesis, states that during any particular year, a bird will produce a smaller clutch than it is physically able to in order to maximize its *lifetime* reproductive output. One reason why a clutch may be smaller than the physiological maximum is due to the overlap of molt and reproduction, which are both energetically costly to the bird. When confronted with a temporal overlap of molt and reproduction, individuals may decrease their clutch size to allow more time and energy for molt (Svensson and Nilsson, 1997). For many migrant species, the breeding season is compressed because they must complete both reproduction and molt before migrating to the wintering grounds (Hemborg et al., 1998).

In this study, I measured the eggs of the second clutch for both weight and length by width dimensions in order to produce some metric of parental investment later in the season, and to perhaps gain insight into the health of the parents as the breeding season ends and migration approaches. The adults experience a conflict late in the season between molt and parental care for the second clutch and are faced with a dilemma of resource allocation. I believe that considerations of life-history traits and strategy molded by evolution via natural selection can aid in understanding the outcome of the second clutch in 2006.

Methods:

Study Site

This study was conducted on Oneida Lake in upstate New York (43° 10'N, 75° 55'W). Oneida Lake is a shallow, predominantly east-west oriented lake with a surface area of approximately 20,000 hectares, and is the largest lake fully contained within the boundaries of New York State. The tern colony is located on Little Island, which is approximately 0.05 hectares and composed of unsorted glacial till ranging from sand and gravel-size elements to larger scattered boulders. Vegetative cover includes: morning glory, cocklebur, tall fescue, and purple loosestrife, that reach a high density by August. Terns commonly colonize two other islands on Oneida Lake during the breeding season, Wantry Island and Long Island, however, no terns nested on Long Island in 2006 and only 21 pairs nested on Wantry, so these data are excluded from this study. The breeding colony on Little Island has a long term data set beginning in 1978 and continuing to the present. The colony is the second largest inland breeding colony of common terns in the U.S., and the numbers typically range from 350-400 breeding pairs each year. The life history and reproductive success of individuals in this colony have been monitored annually by interns under the direction of the New York Cooperative Fish and Wildlife Research Unit (Coleman and Richmond 2003). Trips to monitor and study the colony were made to Little Island contingent upon the weather, ranging from twice a day to twice a week between May 13th and August 13th, 2006.

Nest and Colony Data

To track the progress of each nest throughout the season, a metal stake with orange flagging and an individual nest number was placed into the ground on the periphery of every nest. A census was taken of the colony at least once a week, which included

recording the number of nests and eggs, and aging the chicks when present at a nest. All chicks reaching 10 days in age were assumed to have fledged based on the work of Bollinger (1988), who reports a 95% survival to the fledging stage at 25 days for chicks that reach 10 days in age.

Banding and Adult Trapping

The chicks were banded with a USFWS hard-metal (incoloy) band containing a unique nine-digit number, aged, and the nest was recorded in which they hatched.

In order to assess the degree of philopatry, as well as get an age estimate of the breeding adults, individuals incubating eggs that were seen with bands were trapped on their nests. To trap the adults, we used walk-in mesh traps. A trap composed of mesh netting with a hole in one side was placed over a nest, after which an adult would walk in through the hole and then become trapped inside. Shortly after the adult was inside the trap, we would remove them, record the band number, and then move the trap to another location. This method was quick, precise and caused no harm to any of the trapped birds in this study.

Egg Monitoring and Analysis

The eggs were marked on the shell either as “D”, “E”, or “F” (“G” in two cases) with a number 2 graphite pencil corresponding to the order in which they were laid. Similarly, the 1st, 2nd, and 3rd eggs of the first clutch will be referred to as the A, B, and C eggs, respectively, throughout the remainder of the analysis. These letters required re-tracing every few days due to natural wear on the egg. In order to determine the laying order, I visited the colony every day during this period and checked each nest for new eggs. If

weather did not permit us to visit the colony and laying order was missed, order was determined by weight, the lighter egg being the more recently laid egg. A high precision 100g My Weigh© scale was used to weigh the eggs to the nearest five-thousandth (.005) of a gram. Accuracy and repeatability were achieved by placing the scale inside a plastic cooler to provide a level surface as well as a wind screen while weighing the eggs.

Vernier calipers were used to measure the dimensions of the egg to the nearest 0.1mm at what was determined to be the widest and longest dimensions of the egg. Data collected in 2006 were compared with the data reported by Bollinger (1988) in her master's thesis "Hatching Asynchrony and Factors Influencing Chick Survival in the Common Tern".

Statistics

A one-tailed T-Test was used to compare mean egg weights from groups of samples with different variances; significance was tested for at $p < 0.05$. These tests were run pair-wise, the A vs. D, B vs. E, and C vs. F, to test for weight variation between years, not within clutches. The same test was applied to detect significance between mean numbers of eggs in nests before versus after the flood.

Seasonal Fish Abundance

The fish population numbers were determined by the trawling methodology of sampling, as described in Forney 1974. New techniques to determine fish abundance such as acoustic sampling would give a more accurate measure of fish numbers, but this method was not available on Oneida Lake until 1994, so using this data would give an inaccurate comparison of fish numbers from 1983 and 1984 to 2006.

Results:

Nest and Colony Data

In total, 549 nests were initiated throughout the 2006 breeding season, including both first and second clutch nests; the highest number of nests attended at any one time during the season was 387. Out of the total 549 nests that were initiated, 374 pairs were successful at hatching at least one chick. If we define a successful nest as hatching ≥ 1 chick, 68% of the total nests were successful. These 374 nests produced a total of 930 chicks, or a mean number of 2.49 hatchlings/nest. The number of chicks to fledge was low, 205, or 22% of the total number of chicks to hatch. The average number of eggs in a nest before the flood was 2.57, while after the flood, the average number was 2.08; this difference is statistically significant ($p < 0.05$) (Table 3).

Roughly 10 days after the first flooding event, with sufficient time for the water to recede to its pre-flood level, the island was searched for nest stakes that were no longer marking a viable nest. Nest stakes not associated with a viable nest were assumed to represent a washed-out (destroyed) nest. After collecting the stakes, it was determined that at least 120 nests were washed out during the flood of June 28th. The exact number is not known because some of the stakes from nests that were abandoned prior to the flood were not removed as the nests were abandoned. In the flood recovery effort, 144 pairs made a second nesting attempt. Of the 144 re-nests, only 14% hatched a chick. Two hundred ninety-five eggs were laid in second clutches, of which 47 eggs were known to hatch. Twenty-seven of the hatched eggs were recorded while chicks were still in the nest; an additional 20 chicks were found running loose on the island. More eggs from these nests most likely hatched, but were not counted because the chicks were never

found in the dense vegetation that covered the island at the end of the season. Another 55 eggs were left abandoned at the end of the season for unknown reasons.

Banding and Adult Trapping

Between the 12th of June and the 31st of August, a total of 570 bands were deployed. The majority of bands were placed on chicks, but a few were used to re-band adults whose original bands were worn to the point of illegibility. Twenty-three adults were trapped while on their nests during the 2nd nesting; the average age of a re-nesting adult was 7.21 years, with the oldest individual being 18 years old. Twenty-two other adults were trapped while on their nest before the flood. The average age of a 1st brooding adult was 6.77 years, also having an 18 year old (different individual) as the oldest individual caught on a nest.

From the trapping effort, I also found an instance of what could possibly be double-brooding. During a nest check on June 27th, one day before the flood, nest # 332 with individual 1262-01119 contained one egg and two chicks of age 5 days and 3 days; on July 10th, the same adult initiated a new nest, nest #503. By July 25th, the nest contained two eggs, however, on August 7th, there were zero eggs in the nest. The fate of this individual's chicks is unknown, but it is very possible that this adult and its mate successfully raised some or all of the chicks from the first brood to fledging and then went on to rear chicks from the second clutch to the fledging stage as well.

Egg Monitoring and Analysis

The trendline of the egg weights of the second clutches is very similar to the corresponding trendline of the first clutches, slopes -0.59 and -0.48 , respectively (Figure 1). The mean egg weights for the first clutch of 1983, corresponding to the order in

which they were laid, are as follows: 21.5g, 21.2g, and 20.3g; the weights for 1984 are 21.2g, 21.1g, and 20.5g (Table 4). The mean weights of the 4th, 5th and 6th eggs (second clutch) weighed significantly less ($p < 0.05$) than first clutch eggs at 19.96g, 19.44g and 18.78g, respectively (Table 5). There was a total of 124 D eggs, 85 E eggs, and 21 F eggs measured in 123 nests.

Averaging the two first clutches of 1983 and 1984 together, the differences between the A and D, B and E, and C and F eggs are 1.34g, 1.66g, and 1.62g, respectively. The decrease in the mean egg dimensions within the second clutch also shows a linear decline, the length declining with laying order from 42.07mm to 41.51mm to 39.93mm, and the width decreases from 30.11mm for the D egg, 29.83mm for the E egg, and 29.56mm for the F egg (Figure 2).

Eggs from eight nests were randomly selected in order to determine the amount of water loss due to evaporation during the incubation process. Through the analysis of 15 eggs, it was determined that egg weight decreases by .088g/day due to water evaporation as the embryo grows (Figures 3a,b, and c). I was not able to weigh many eggs at the exact time of hatching, however, I was able to weigh two of the randomly chosen eggs at the time that they hatched, and it is interesting to note that there is a large decrease in the weight of these two eggs right before hatching that probably happens when the chick pips and creates a hole in the egg.

Seasonal Fish Abundance

The numbers of larval perch (young-of-the-year, age 0) greatly decreased in all three seasons from June to August (Table 6). For example, on June 18th in 1983, there were 45,600 young-of-the-year perch, but on August 1st, there were only 9,600 fish, and 664

on October 15th. The difference was even more dramatic in 2006, going from 58,500 on June 8th to 1,544 on August 1st to 240 on the 15th of October. Because of the sampling technique, these numbers do not reflect the absolute number of fish in the lake, but they do give relative numbers.

Discussion:

The speculations made in this paper rely heavily on the assumption that little has changed in the Oneida Lake study system between 1983 and 2006 in terms of the environment and physiological requirements and conditions of the birds. Specifically, some environmental conditions may have changed to affect the lake, and the individual birds of this study are very unlikely the same birds that Patricia Bollinger studied in 1983, but these changes are assumed to be insignificant. The fact that nesting efforts, clutch size, and fledging rates are nearly the same is evidence that the two data sets can be compared because enough similarity has remained in the study system to allow for realistic comparisons.

Considering this, the egg weights of the second clutch were significantly less than the corresponding eggs of the first clutch. The graphical comparison of the three clutches (two first clutches from 1983 and 1984 and one second clutch from 2006) can be seen in Figure 2. The differences from the A to D, B to E, and C to F eggs are 1.34, 1.66, and 1.62 grams, respectively. It has been shown that there is a seasonal decline in the reproductive output of birds with strictly defined breeding seasons (Price et al. in Arnold et al. 2004). Arnold et al. (2004) argue that this decline is due to one or a combination of two factors: the time at which the brood is started, and/or the quality of the parents. However, they concluded from their experimental manipulations that it was a

combination of both parental quality and the timing of breeding that led to the seasonal decline in breeding success. The Arnold et al. study is one of experimental manipulation of nests in the earlier part of the season (until June 9th), whereas this study involved no manipulation, rather it was an observational study of natural occurrences. Therefore, it is difficult to say with certainty which factor(s) contributed to the lower egg weights of the second clutch. Although it was not empirically proven, two proximate factors are likely accountable for the decline in reproductive success: a decline in food resources and physiological stress of the adults, which will be discussed below. It does seem apparent that the lay date did have an effect on the outcome of the second clutch. Starting in middle July, breeding adults were much less likely to attack researchers on the colony (as compared to late May and all of June), indicating that their interest in reproductive activities had largely declined later in the season. The number of young to fledge from second broods was not recorded, but to further exemplify the decline in reproductive interests, 55 eggs were left abandoned in nests at the end of the season. Considering a total of 144 pairs that re-nested, and a mean clutch size of 2.08 eggs, this equates to 18% of the total number of eggs in second clutches.

A second, equally plausible hypothesis is that the eggs of the second clutch will in fact weigh more than the eggs in the first clutch. The reasoning behind this is that the birds lay the first clutch within a couple weeks of arrival at the breeding grounds after a long return journey from their wintering grounds in either Central or South America, which means energy reserves might be low. On the other hand, the majority of the second clutches were laid in early-mid July, approximately two months after their arrival from migration. During the early part of the season, food such as emerald shiners

(*Notropis atherinoides*) and yellow perch (*Perca flavescens*) is quite abundant, and flights are typically limited to short foraging trips on the lake. These two factors would make it seem that the birds should have as much, if not more energy to put into a reproductive effort later in the season, but if egg weights indicate the relative health/condition of the parents, this is not the case. I will now attempt to reconcile the data from 2006 with already existing hypotheses, as well as add some new explanations, in an effort to address why the eggs of the second clutch weighed less than the first clutch, and in turn, why the second nesting attempt was largely unsuccessful.

Brood-reduction, Brood-survival, and Insurance Hypotheses

The slope of the lines on the graph representing laying order vs. egg weight (Figure 2) is very similar between the first and second clutches, showing that even later in the season, the birds show the same decline in egg weights within the clutch. Many studies have been conducted concerning the intraclutch variation of egg weights amongst birds (Slagsvold et al. 1984, Viñuela 1997, Aparicio 1999, Rafferty et al. 2005), including some that focus on larids and sternids (Gochfeld 1977, Meathrel and Ryder 1987). As discussed before, it is believed that there is an ultimate, adaptive significance to intraclutch variation in egg sizes. Birds that lay eggs of decreasing weight with the final egg weighing the least, such as terns, are most likely to follow the brood-reduction or insurance hypothesis, while birds that lay a relatively large final egg are most likely to fit the brood-survival hypothesis (Clark & Wilson, 1984).

The brood reduction hypothesis is elucidated when examining cases of asynchronous egg-laying. Common terns lay eggs successively, typically one egg per day for three days. The parents begin incubating immediately after the first egg is laid,

which generally means that the first egg laid is also the first to hatch, setting up a hierarchical division of size amongst the chicks. Because the last laid egg weighs the least in the clutch and hatches on average two days after the first egg, one might expect that this chick will die due to resource competition amongst siblings. A study conducted by Nisbet (1973) supported this hypothesis, that there is indeed a decreased survival of the last-hatched chick in the common tern due to sibling competition. It is therefore deemed adaptive because this maximizes the number of offspring that the parents are able to rear with varying environmental conditions.

During 2006, many of the E or F eggs, whichever was last in the clutch, failed to hatch. The brood-survival hypothesis does not apply here because the last laid egg in the common tern is relatively smaller than the preceding eggs. Also, the insurance hypothesis cannot explain the data because under this hypothesis, all of the eggs must hatch. However, the brood-reduction hypothesis could explain the abandonment at the end of the season. This hypothesis attempts to explain why the last-hatched chick dies due to a size difference amongst siblings, but I suggest that this hypothesis could be extended to apply to the eggs of a clutch as well. The eggs that didn't hatch at the end of the season failed because of a decreased level of parental effort due to the late initiation of the second clutch and change in environmental conditions. Parental effort decreased in either the form of the production of a low quality egg or poor incubation; it is possible that there is some weight threshold under which eggs are inviable and simply do not hatch. In either case, the brood was reduced because the resources necessary to successfully raise, or in this case hatch a chick, were low.

Proximate vs. Ultimate Causation

A proximate cause is the immediate, often physiological, mechanistic, or environmental cause that explains an occurrence. The decreased egg weight of the second clutch could be attributed to two proximate causes in particular. During and after the flood, much debris and sediment was stirred up in the lake, making waters turbid. The method terns use for feeding is termed “plunge diving”, which involves a controlled dive from some height above the water after they have spotted a fish. The turbid water during and after the flood could have created difficult foraging conditions, meaning fewer fish were consumed and the condition of several adults may have temporarily declined during the stage of egg formation. The second cause of the decreased egg weight is the physiological stress that the birds encountered during the flood. Various stressful stimuli, severe weather in particular (Wingfield 1988), have been shown to increase corticosterone levels in birds (Silverin et. al 1997). Corticosterone plays an important role in coordinating physiological and behavioral changes, such as the suppression of territorial and reproductive behaviors (Silverin et. al 1997). Examples of such behaviors include increased foraging and “dread flights”; elevated levels of corticosterone are likely to inhibit reproductive activities and instead, behaviors are redirected towards ‘survival’ (Silverin et. al, 1997). The elevation of corticosterone levels in the adults due to the flood could have ultimately caused an abandonment of breeding territories as their behaviors became less focused on reproduction and more focused on survival activities such as molt and increased foraging to build fat stores for migration.

In addition to the aforementioned proximate causes, ultimate factors must be considered as well when examining reproductive strategies. Ultimate causes explain

phenomena from a historical perspective, as the evolutionary reason why something is the way it is. Invoking ultimate causes helps explain the evolution of clutch size. Individuals within a species show variation in clutch size, some laying two eggs and some laying four eggs, etc. Natural selection will favor the individual that produces the most offspring throughout its entire lifetime, not the individual that produces the highest number of offspring in any one season. Lack's hypothesis, which takes into account the fecundity of the parents, states that any individual will produce a brood slightly smaller than they are physically able to produce, a result of ultimate causation. This was exemplified by Nager et al. (2001) who showed that increasing the egg production in lesser black-backed gulls (*Larus fuscus*) caused a fitness reduction in experimental individuals during the following year of the study. At the end of the 2006 breeding season, many adult terns on Oneida abandoned their eggs and chicks. Invoking Lack's hypothesis, this abandonment happened because the adults experienced a conflict of interest between reproduction and survival, and because these individuals are the products of evolution selected to maximize their reproductive output, the adults abandoned the eggs in order to survive to reproduce in the next season. In order to survive to the next season, the birds must finish their molt before the fall migration.

Timing vs. Parental Quality Hypotheses, and Life-History Conflicts with the Production of a Second Clutch

One reason for the reduced parental care in the current study under the timing hypothesis is the decreased level of breeding synchrony that occurred after the flood. As Figure 4 shows, there were two distinct peaks of nest initiation during 2006, the first, composed of one in the beginning of the season and the second peak shortly after the flood that

occurred on June 28th. Individuals continued to initiate nests through the end of July, and as can be seen in Figure 4, the final 42 nests (29% of re-nests) were laid over a 17-day span. This interval appears to be small, but in the same time interval in the beginning of the season, at least 350 nests were initiated, exemplifying the disparity in breeding synchrony between the early and later times of the breeding season.

A second piece of supportive evidence for the timing hypothesis explaining the diminishment in reproductive success is the declining number of fish found in Oneida Lake throughout the season. During the summer of 2006, the number of yellow perch per hectare of lake surface decreased approximately 40 times (Table 6). Although yellow perch do not constitute a majority of the common tern's diet, they are consumed on a regular basis. The most common prey item in a common tern diet on Oneida Lake is the emerald shiner, but the data for this species is not available for Oneida Lake. It is known, however, that the number of larval fish of every species decreases as the season progresses due to predation by larger fish and birds, so that the number of fish that terns are capable of handling decreases later in the season. This decrease in the number of fish to prey upon, and the decrease in breeding synchrony as the season progressed (particularly after the flood) support the timing hypothesis in explaining the decline in reproductive success of the 2006 season. As mentioned earlier, not enough data were taken in order to test the parental quality hypothesis.

Molt and reproduction do not normally coincide because both are energetically costly (e.g. Williams 1966; Lindström et al. 1993). If an overlap occurs between reproduction and molt, there will likely be a trade-off between the energy and time required for each (Hemborg et al. 1998). From late June through early August, many

feathers were found on Little Island, indicative of molt. The second nesting attempt occurred throughout the entire month of July, overlapping with a substantial portion of the molting phase. Svensson and Nilsson (1995) created a similar experimental situation on the blue tit (*Parus caeruleus*) in which they induced a late repeat clutch that coincided with molt. This experiment produced some important results that bear great significance on the current study: 1.) females that initiated a second breeding attempt laid significantly fewer eggs than in their first clutches, 2.) a higher proportion of experimental (molting) males molted while feeding nestlings as compared to control (non-molting) males, 3.) experimental males contributed significantly less feedings to their brood than did control males, and 4.) experimental broods suffered higher levels of nestling mortality. These results can in turn be applied to this study.

During a typical year when only a single brood is produced, molt occurs after the energy-intensive phases of egg production, incubation, and chick rearing. However, during this year the production of the second clutch coincided with molt. From the experiment of Svensson and Nilsson, we would expect to see fewer eggs in the second clutch, fewer feedings to their brood by molting individuals, and higher levels of nestling mortality and egg abandonment. I did not measure the number of feedings or levels of nestling mortality, but I did record the number of eggs, and in fact, there was a lower mean number of eggs in second clutches than in first clutches (Table 3). In addition to the findings of Svensson and Nilsson, Heaney and Monaghan (1996) hypothesize that the success of a breeding attempt is dependent upon how the parents allocate effort between the phases of reproduction, i.e. egg production, incubation, and chick rearing. They also demonstrated that the costs of incubation alone can greatly decrease parental performance

later during the same breeding attempt. According to these two studies by Svensson and Nilsson and Heaney and Monaghan, the terns produced fewer eggs in the second clutch that weighed less than eggs of the first clutch because the adults were molting while producing the second clutch and also because they lost additional energy due to the costs of incubation. We can further explain the outcome of the second nesting attempt if we examine the allocation of parental effort during the chick rearing phase.

Common terns exhibit bi-parental care, with each parent performing a more or less equal share of the costs of chick rearing (post egg-laying), a commonality of many monogamous species. During incubation, one adult attends the nest while the other is foraging (Langham 1972). While one incubates, the other forages for both itself and its mate, and upon return to the nest with a fish, the pair often engages in pair-bonding displays. Once the chicks have hatched, both parents share foraging responsibilities to feed the young. This aspect of tern life history conflicted with the production of the second clutch because some of the pairs that re-nested were simultaneously feeding the chicks from the first clutch, and incubating the eggs of the second clutch. This creates a situation where one adult is foraging for itself, its mate, and <3 rapidly growing nestlings with high nutritional demands. This observation is another potential reason why the vast majority of second clutches failed.

Conclusion

What seemed to be a simple question regarding the difference in egg weights between first and second clutches turned out to have an involved answer. The components of the answer ranged from proximate and physiological effects to evolutionary strategies molded through natural selection. It proved important to consider not only the

hypotheses concerning intraclutch variation in egg weights, but also the hypotheses that attempted to explain the decrease in reproductive success as the season progresses, in answering this question. Reduced breeding synchrony and the decline in populations of small fish created sub-optimal conditions under which to rear the second clutch. Molt, an energetically costly activity, expended energy that would have been necessary in successfully raising a second clutch.

Testing hypotheses in the field is difficult, especially when the study is non-manipulative. It is the biologist's greatest asset to be able to formulate novel questions from unpredictable events that otherwise might not have been addressed. This study is the product of such a stochastic event, and although certain questions were addressed, many more are raised. But perhaps this should be an ulterior motive of a scientific study, not only to address current questions, but also to raise further questions for studies in the future.

Future Studies and Notable Observations:

This study offers possible insight into the production of second clutches in seabirds, but not enough data were taken to accept or refute the discussed hypotheses. During the analysis phase of this study, many thoughts have crossed my mind that would make this a more complete study. Most of these suggestions are valid for any study, but some are pertinent only to Oneida Lake.

I believe the production of a second clutch is more common than suspected in published literature. What confounds this observation is that pairs that double clutch are most likely caring for the chicks of the first clutch at the same time as incubating the

chicks from the second clutch. Individuals that raise two broods must complete both bouts of reproduction before initiating molt in order for both broods to be successful. With a temporally compressed breeding season, overlap between the first and second broods will occur. It follows that my suggestion to the researcher is to pay careful attention to the reproductive activities of the adults, and perhaps somehow mark the eggs of the first clutch so as not to get fooled by missing the initiation of a second clutch shortly after the hatching of all the eggs in the first clutch. It is also imperative to follow the fate of the chicks when a second clutch is observed. Due to time constraints, I was not able to monitor the colony after mid-August, but if these data were collected, conclusions could have been made with greater certainty. Another question that a future study could address is whether or not there is some minimum egg weight that is necessary to produce a hatchling. It is possible that an egg simply will not hatch if it is below a certain weight when it is laid.

In addition to these broader questions, this study also provides some interesting questions that can be addressed during the summer of 2007 on Oneida Lake. For instance, what is the total number of chicks to fledge during 2007 as compared to previous years? Another really interesting question is to examine the reproductive success in 2007 of the 23 individuals that were trapped on nests after the flood. This would be easily done considering that I have the band numbers of these individuals. These questions will address the fitness effects of a second clutch on the reproductive success of these individuals during the following year.

Notable Observations

While taking data on the island, a few unusual behaviors were observed. First, an adult was observed feeding a >10 day old chick a dragonfly. A tern's diet is composed mainly of fish, and it was not observed whether the dragonfly was caught on the water or out of the air, but this is unusual behavior either way. Secondly, the nest of a female mallard (*Anas platyrhynchos*) on Little Island was also washed out during the same flood on June 28th. This female was observed on more than two occasions to be giving some sort of "parental care" to some tern chicks. She was never witnessed to feed them, but she seemingly was directing them where to go while swimming behind them, and letting them lay on and with her on her nest. This behavior was observed on more than one occasion, but it is unlikely that she was caring for the same chicks each time. This strange behavior was most likely due to the female's "broodiness", or propensity to care for a brood towards the end of incubation. Lastly, I noticed an incident of cannibalism. Cannibalism amongst terns is rarely documented (Zubakin, 1975), and is associated with times of high stress amongst the colony. Less than a week after the flood, with water levels still high, I observed a juvenile (≥ 10 days) trying to swallow whole another juvenile, approximately ≤ 2 days. The chick being eaten was about half way down the older chick's mouth, the posterior end still sticking out. I was not on the island long enough to see if the chick was swallowed, and I also never saw the cannibalistic chick again, so exactly what happened to it after this event is unknown.

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Tables & Figures:

Table 1—A brief summary of the clutch sizes, relative size of last laid egg, and mean egg volume of several passerine and non-passerine species, from Slagsvold et al. 1984.

Species	Clutch Size	Relative size of Last Egg (%)[*]	Mean Egg Volume (cm³)
<i>Eudyptes chrysolophus</i>	2	24.31	114.32
<i>Eudyptes robustus</i>	2	12.87	102.16
<i>Sylvia atricapilla</i>	4	7.93	2.03
<i>Emberiza schoeniclus</i>	4	7.82	1.93
<i>Turdus iliacus</i>	5	6.13	4.95
<i>Luscinia luscinia</i>	5	5.06	2.54
<i>Tachycineta bicolor</i>	5	3.76	1.86
<i>Turdus pilaris</i>	5	3.66	6.81
<i>Quiscalus quiscula</i>	5	3.5	6.58
<i>Troglodytes aedon</i>	5	2.75	1.41
<i>Calidris minutilla</i>	4	1.36	6.54
<i>Phalacrocorax aristotelis</i>	2	0.92	48.75
<i>Parus major</i>	11.9	0.91	1.74
<i>Megadyptes antipodes</i>	2	-0.28	129.75
<i>Larus novaehollandiae</i>	2	-1.09	38.65
<i>Sterna hirundo</i>	3	-1.33	20.09
<i>Larus marinus</i>	3	-1.8	101.36
<i>Sterna dougallii</i>	2	-2.26	19.95
<i>Branta canadensis</i>	3.89	-2.53	138.64
<i>Pygoscelis adeliae</i>	2	-3.4	108.24
<i>Larus ridibundus</i>	3	-3.66	34.73
<i>Larus californicus</i>	3	-4.13	72.58
<i>Larus atricilla</i>	2.79	-4.18	42.57
<i>Aquila verreauxii</i>	2	-4.33	99.83
<i>Larus delawarensis</i>	3	-4.65	51.78
<i>Pygoscelis papua</i>	2.19	-4.71	123.91
<i>Corvus corone</i>	4	-5.33	19.29
<i>Larus fuscus</i>	3	-6.29	71.25
<i>Larus argentatus</i>	3	-6.48	91.23
<i>Hieraaetus fasciatus</i>	2	-11.72	97.89

* Deviation (in %) of the size of the final egg laid from that of the mean size of all the eggs in the clutch.

Table 2—Comparison of the relative size of the final egg laid for distinct groups of passerines and non-passerines, from Slagsvold et al. 1984.

Species Group	Number of species	Mean Deviation (%)*
Non-passerines		
Precocial	9	-0.68
Altricial	19	-3.91
Passerines		
Hole-nesters	13	-0.05
Open-nesters	17	3.56

* Deviation (in %) of the size of the final egg laid from that of the mean size of all the eggs in the clutch.

Table 3—The average number of eggs per nest before and after the flood; sample sizes in parentheses.

	Mean Number of Eggs	Standard Error
Pre-Flood	2.58* (425)	0.03
Post-Flood	2.08* (144)	0.06

*Significance level $p < 0.05$

Table 4—Average egg weights from the 1983 and 1984 breeding seasons including standard deviation, as collected by Patricia Bollinger; sample sizes are in parentheses.

Mean Egg Weights From 1983 and 1984			
	A	B	C
1983	21.5±1.6 (105)	21.2±1.4 (105)	20.3±1.8 (105)
1984	21.2±1.6 (130)	21.1±1.5 (130)	20.5±1.5 (130)

Table 5—The average egg weights of the D, E, and F eggs of the 2006 breeding season including standard deviation, sample sizes in parentheses.

Mean Egg Weights From 2006		
D	E	F
19.96*±1.55 (124)	19.44*±1.25 (85)	18.78*±1.45 (21)

*Significance level $p < 0.05$

Table 6—Numbers of young-of-the-year perch (age 0) for various times during the 1983, 1984, and 2006 seasons; numbers represent number of fish per hectare of lake surface area.

Year	Larval Survey	1-Aug	15-Oct
1983	45,600 (June 18)	9,600	664
1984	16,000 (June 17)	5,030	896
2006	58,500 (June 8)	1,544	240

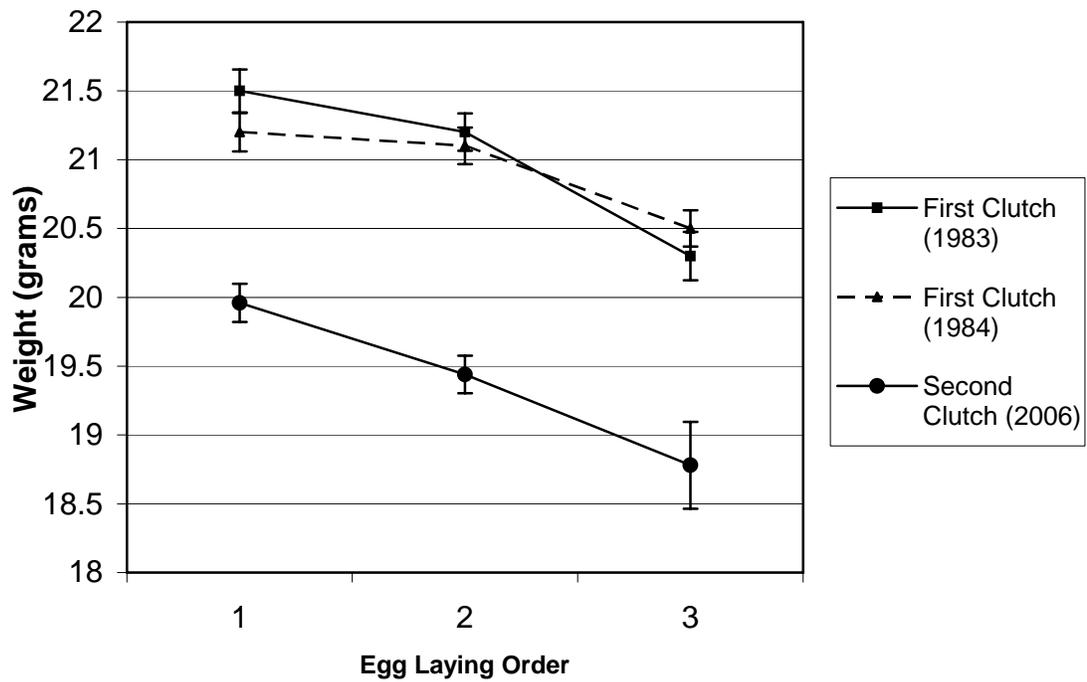


Figure 1. Comparison between mean egg weights of the first broods of 1983 and 1984 (egg weights of the two years averaged together) with the mean egg weights of the 2nd brood of 2006; standard error bars are shown.

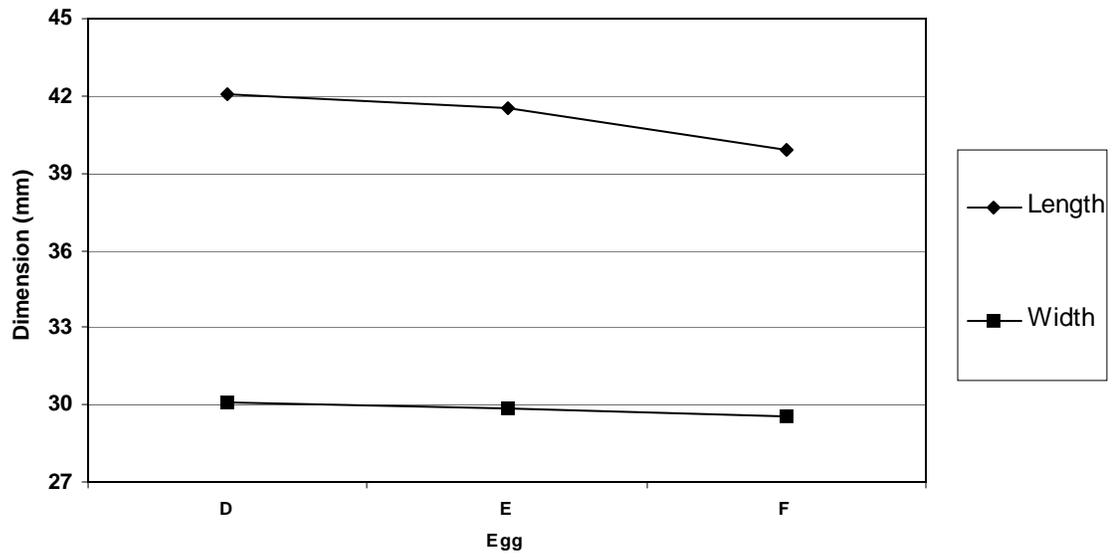


Figure 2. The average widths and lengths of the D, E, and F (second clutch) eggs of the 2006 breeding season.

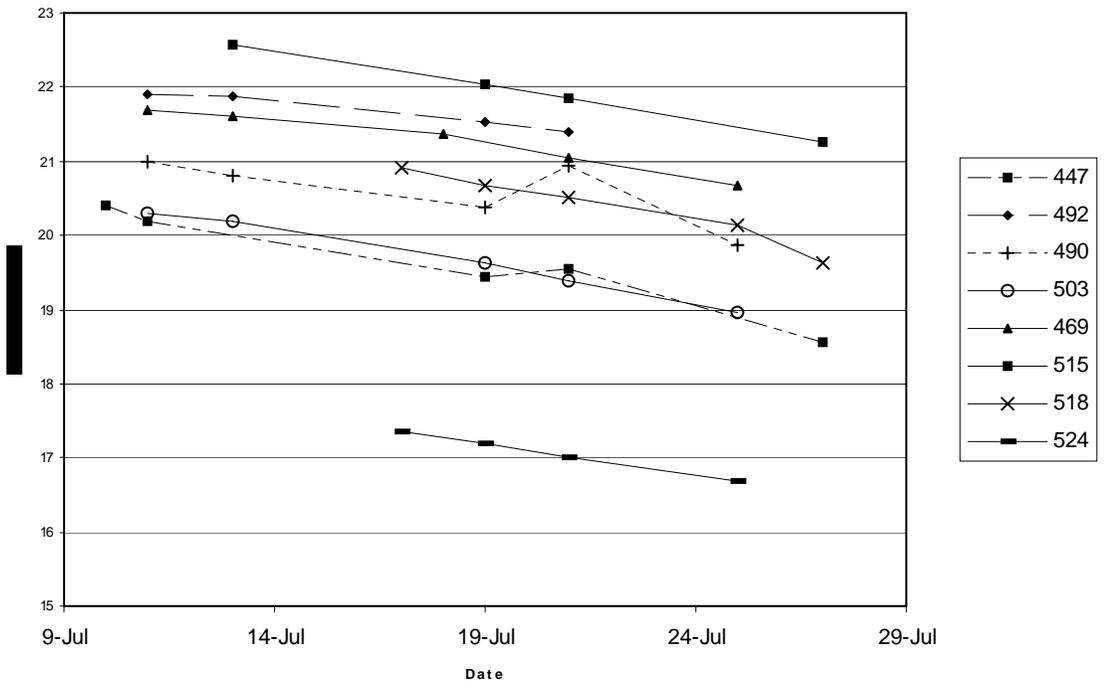


Figure 3a. Egg weight loss of the D egg due to evaporation during embryo development in 2006 of eight randomly selected nests.

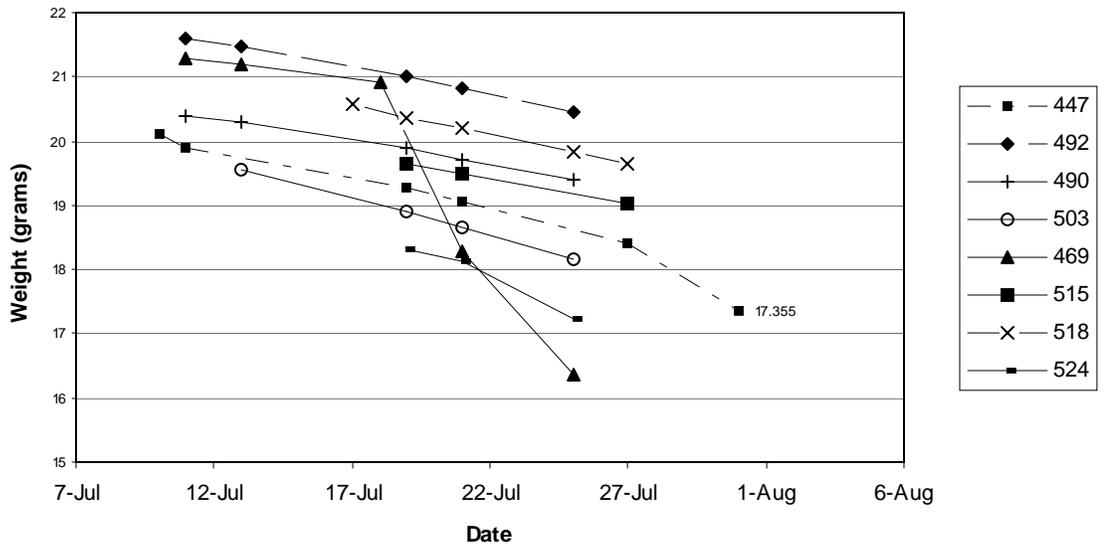


Figure 3b. Egg weight loss of the E egg due to evaporation during embryo development in 2006 of eight randomly selected nests. Nest 447 hatched an egg that weighed 17.355 grams upon hatching. The egg of nest 469 is an outlier and may have been cracked during the incubation period.

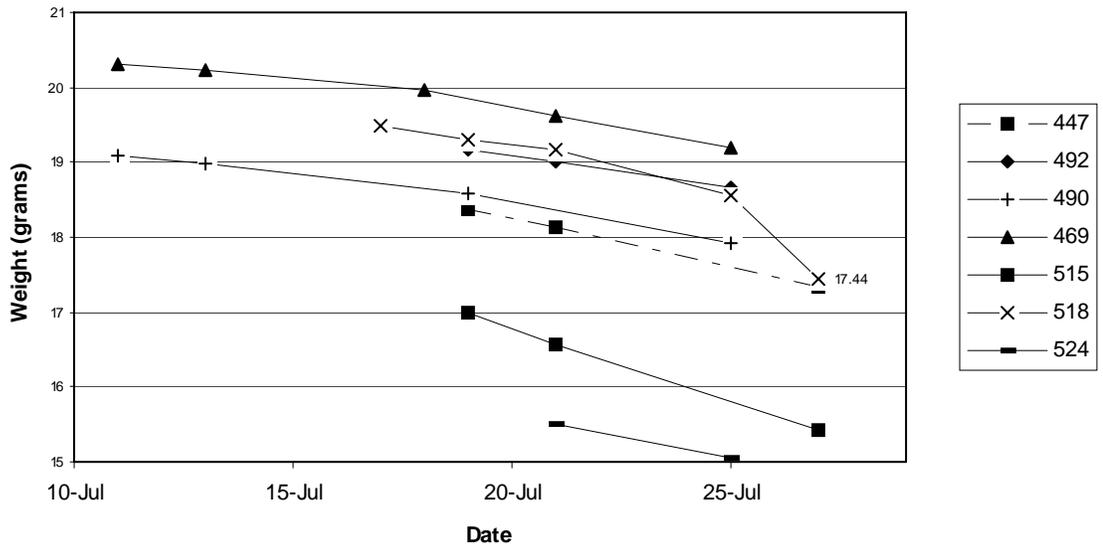


Figure 3c. Egg weight loss of the F egg due to evaporation during embryo development in 2006 of eight randomly selected nests. Nest 518 hatched an egg that weighed 17.44 grams upon hatching. Nest number 503 produced only two eggs so it does not appear in this graph.

Nest Initiation vs. Date

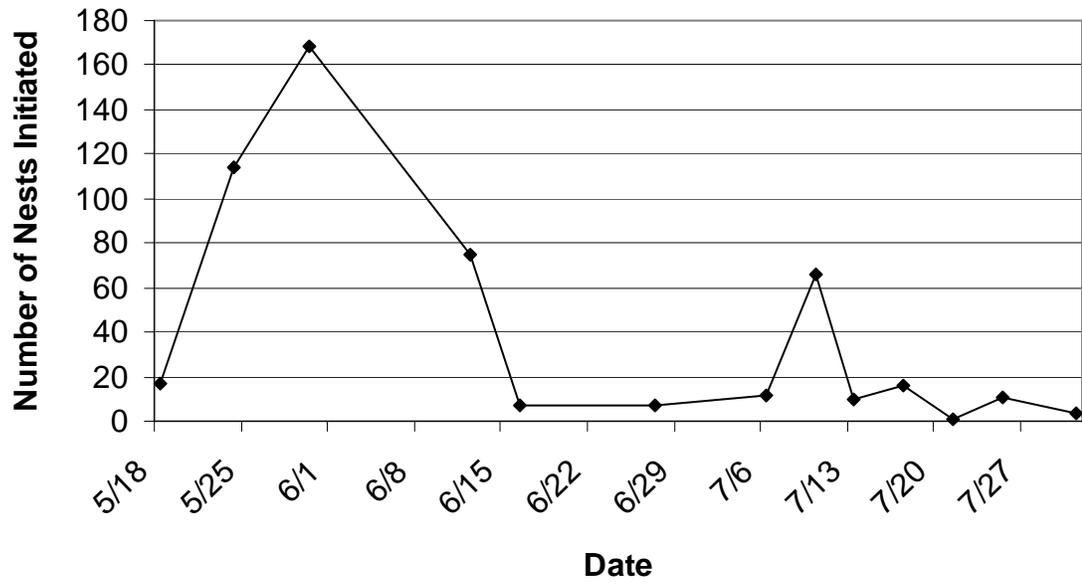


Figure 4. Number of nests initiated by date in the 2006 breeding season; the flood occurred on June 28th.