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Age-Specific Reproductive Effort in Leach's Storm-petrels, *Oceanodroma leucorhoa*

By Emily Balf '05, advised by Dr. Bob Mauck



Abstract

Leach's storm-petrels exhibit reproductive behavior that changes as they age. In 2004 the mean length of eggs was 32.6; the mean width was 23.6; the mean egg volume was 9.289. Egg volume did not change significantly from 1991 to 2004 when looking at the whole population. Female size does not have a significant effect on egg volume. Female Leach's storm-petrels do not appear to allocate more energy to reproduction as they age. This favors the selection hypothesis.

Introduction

It is widely known that reproductive success/performance often improves with birds as they age (Forslund and Pärt, 1995), and age-related reproductive behavior has been documented in this population of Leach's storm-petrels (Mauck et al., 2004). There are three hypothesis that could explain age-related reproductive success: progressive appearance or disappearance of phenotypes, age-related improvements of competence, and optimization of reproductive effort—more succinctly called the selection, experience, and effort hypotheses respectively (Forslund and Pärt, 1995).

Leach's storm-petrels are an excellent study species when asking questions of life history decisions and trade-offs as the behavior of individuals can be analyzed over many years due to their long life and breeding philopatry. The population on Kent Island has been monitored by C.E. Huntington since 1955. Such a long-term demographic study is a valuable resource for our understanding ecological and evolutionary processes (Wheelwright and Mauck, 1998). Due to these factors, some birds studied by Mauck in 1991 are still alive and breeding.

With a population as well documented as this, two types of studies are possible, latitudinal and longitudinal. A latitudinal study would compare behavioral differences exhibited between old and young birds within the population measured in a given year. A longitudinal study would compare behavioral differences exhibited by an individual across years of measurement. Due to the abundance of data on this population over a period of 50+ years, a longitudinal study was possible. Comparisons were drawn between individuals measured both in 1991 and 2004.

Egg size can be used as a measurable indicator of age-related reproductive behavior. Egg size is a concrete measurement of reproductive effort in that it represents energy directly allocated to the offspring by the female. Egg size has been shown to be related to reproductive success in other procellariiforms (Weimerskirch, 1992). The selection hypothesis predicts that individuals breeding in 1991 and 2004 should show no difference in these measures between years (adjusted for annual differences relative to the population as a whole). Both the effort and experience hypotheses predict and increase in egg size with age.

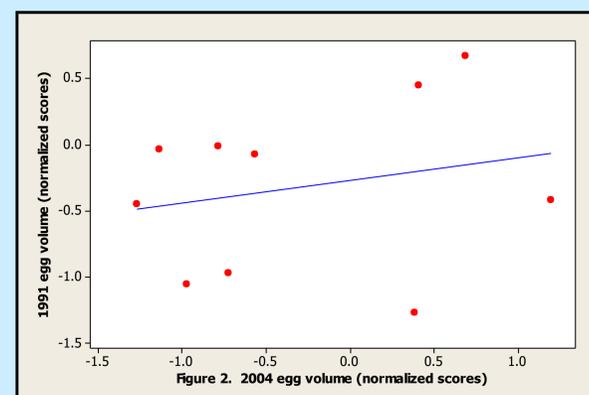
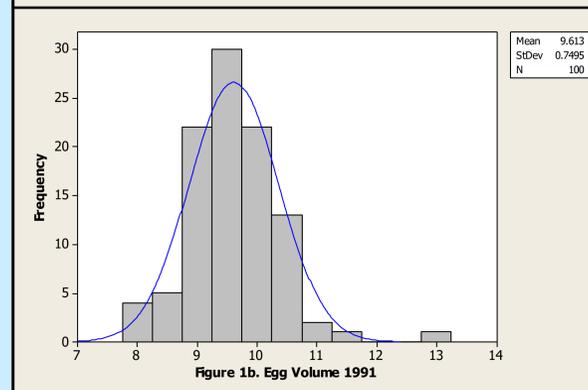
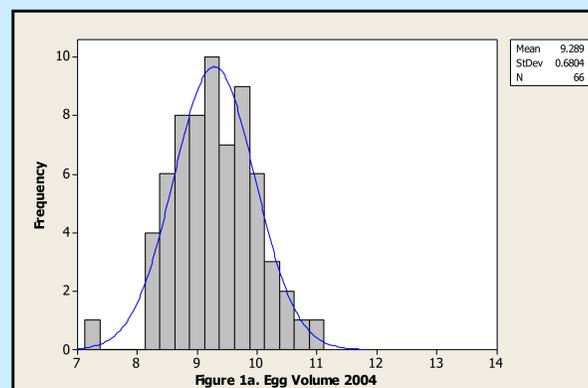
Materials and Methods

Kent Island is a small island in the Bay of Fundy off of the coast of New Brunswick, Canada (44°35' N, 66°45' W). Approximately 2200 pairs of Leach's storm-petrels (*Oceanodroma leucorhoa leucorhoa*), breed yearly on this island. Leach's storm-petrels are a long-lived pelagic seabird of the order Procellariiform, breeding up to 35 years. They dig burrows in the ground where they lay and incubate one egg per breeding season (Huntington et al., 1996). Of the 100 females measured in 1991, 10 were recaptured and measured, along with their eggs, in 2004. Measurements, both of the birds and the eggs, were obtained by manually removing the bird from the burrow in the daytime while it is incubating.

Only burrows where female wing and tarsus and egg length and width were measured were used for analysis. Wing and tarsus measurements were used to standardize egg volume by size of female. I measured wing length (mm) using a large wing ruler. I measured the tarsus (mm) of the right leg using a Vernier caliper. In the cases where the right leg was clearly damaged or missing, the left tarsus was measured. Egg length and width were measured using the same Vernier caliper. Egg measurements were used to calculate volume using the equation developed by Huntington et al. (1996):

$$\text{Volume} = (0.512) * \text{Length} * (\text{Width}^2/1000)$$

Normal scores were used in comparisons between years to standardize for ecological factors and measurement techniques. Analysis was done using Minitab 14.



Results

Egg length, width and volume were normally distributed, thus parametric statistics could be used. No correlation was found between tarsus length and egg volume for either 1991 or 2004 (1991 regression equation: Volume = 7.95 + 0.067 Tars, t-value = 0.52, p = 0.61, 2004 regression equation: Volume = 5.41 + 0.156 Tars, t-value = 1.51, p = 0.14). Raw egg size was significantly different between 1991 and 2004 when comparing the whole population (two sample t-test, $N_{91} = 100$, $N_{04} = 66$, T-Value = 2.88, p = .005, Figs. 1a, 1b, Table 1). Egg volume was greater in 1991 than 2004 for the population as a whole. Eggs of females caught both in 1991 and 2004 showed decreases in all dimensions in 8 out of 10 individuals (Table 2). Raw data from 1991 and 2004 show that egg size decreased for the entire population from 1991 to 2004. Both raw egg dimensions and standardized scores for egg volume of individuals measured in both 1991 and 2004 showed no significant change from 1991 to 2004 (paired t-tests, N= 10 for 1991 and 2004 in both raw and standardized, raw: t-value = 2.20 p-value = 0.056, standardized: T-Value = -0.12 P-Value = 0.904, Fig. 2). The ratio of length/width did not change significantly between 1991 and 2004 (regression equation: $l/w_{04} = 0.253 + 0.822 l/w_{91}$, t-value = 1.96, p = 0.85).

Year	N	Length (mm)	Width (mm)	Volume (cm ³)
1991	100	33.0 ± 1.1	24.0 ± 0.7	9.6 ± 0.8
2004	66	32.6 ± 1.1	23.6 ± 0.7	9.3 ± 0.7

Table 1. Raw egg size comparisons. 2 sample t-tests, for all tests $N_{91} = 100$, $N_{04} = 66$, width: t-value = -3.44 p-value = 0.001, length: t-value = -2.19 p-value = 0.030, volume: t-value = 2.88 p-value = 0.005

Year	N	Length (mm)	Width (mm)	Volume (cm ³)
1991	10	32.9 ± 0.76	23.8 ± 0.33	9.5 ± 0.35
2004	10	32.5 ± 0.81	23.4 ± 0.68	9.1 ± 0.59

Table 2. Raw egg size comparisons for individuals measured both in 1991 and 2004. Paired t-tests, for all tests $N_{91} = 10$, $N_{04} = 6$, width T-Value = -2.26 P-Value = 0.050, length T-Value = -2.24 P-Value = 0.052, volume T-Value = 2.20 P-Value = 0.056

Discussion:

All of the analyses provide evidence to support the selection hypothesis. The selection hypothesis predicts that there will be no change in relative reproductive effort over time, as individuals are selected for based on phenotype. Thus a bird that survives and breeds for 14 successive years should show no change in egg size from the first breeding year to the last (Mauck et al. 2004). There was a significant difference in egg size from 1991 to 2004 when comparing the general trend for the populations of both years. Two possible explanations for this are, 1. that ecological conditions such as harsh weather or food availability affected egg production, thus limiting or increasing size, or 2. that measurement methodology changed from 1991 to 2004, though we did standardize for that and within years there was no significant difference based on who did the measurement. Further studies looking at a larger sample size with more intermittent years may be able to determine whether or not the progression of egg size is truly insignificant. However, it is necessary to note how rare it is to have a data set this complete for such an extended period of time. I am also curious to see whether this trend is true for all Procellariiforms.

Literature Cited

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