*Evolutionary Ecology Research*, 2011, **13**: 19–33

# Male-biased reproductive effort in a long-lived seabird

Robert A. Mauck[1], Jennifer L. Zangmeister[1], Jack C. Cerchiara[1],
Charles E. Huntington[2] and Mark F. Haussmann[1]

[1]*Biology Department, Kenyon College, Gambier, Ohio, USA and*
[2]*Biology Department, Bowdoin College, Brunswick, Maine, USA*

## ABSTRACT

**Background:** In dimorphic seabirds, the larger sex tends to provision more than the smaller sex. In contrast, monogamy and biparental care are often associated with equal effort between the sexes. However, the few studies that have tested sex-specific effort in monomorphic seabirds have primarily examined the details of foraging at sea.

**Hypotheses:** Parental effort is also sex-biased in a monomorphic seabird mating system for one of two reasons: (1) If females enter the period of parental care less able to invest in care due to the cost of egg production, male-biased effort may be necessary to avoid reproductive failure. (2) Alternatively, female-biased effort may occur due to the initial disparity in gamete size, particularly in species with internal fertilization.

**Organism:** Leach's storm-petrel (*Oceanodroma leucorhoa*), a monomorphic seabird with true monogamy and obligate biparental care.

**Site:** A breeding colony of *Oceanodroma leucorhoa* at the Bowdoin Scientific Station on Kent Island, Bay of Fundy, New Brunswick, Canada.

**Methods:** Across multiple breeding seasons, we assessed incubation behaviour and chick-rearing behaviour through one manipulative and multiple observational studies. We assessed energetic investment by inducing feather replacement and measuring the resulting rate of feather growth during both the incubation and chick-rearing phases of parental care.

**Conclusions:** We observed male-biased effort. Males incubated the egg for a greater proportion of time than did females and, when faced with an egg that would not hatch, males continued to incubate past the point when females abandoned it. Males made a higher percentage of total food deliveries to chicks than did females, resulting in greater mean daily food provisioning by males than by females. During chick rearing, males grew replacement feathers more slowly than did females, indicating that males were more likely to reduce their own nutritional condition while raising chicks than were females. These results support the hypothesis that females enter the period of parental care at a nutritional deficit and males must compensate to avoid reproductive failure.

*Keywords*: life-history trade-offs, parental effort, ptilochronology, sex-specific reproductive effort.

---

Correspondence: R.A. Mauck, Biology Department, Kenyon College, Gambier, OH 43022, USA. e-mail: mauckr@kenyon.edu

## INTRODUCTION

That reproduction is costly is a central tenet of life-history theory (e.g. Williams, 1966) and the trade-offs between fecundity and survival experienced by birds are well documented (e.g. Ghalambor and Martin, 2000, 2001; Ardia, 2005; Paredes *et al.*, 2005). Costs associated with one breeding season may negatively impact future reproduction (Lindén and Møller, 1989; Milonoff *et al.*, 2004) and the raising of young is often considered the most costly reproductive investment made by birds (Monaghan and Nager, 1997).

Levels of parental investment by males and females often differ (Trivers, 1972). In most birds, females provide the majority of parental care, particularly in those systems in which male–male competition has selected for relatively greater male investment in mate acquisition rather than parental care. The role of male care in monogamous avian mating systems ranges from systems in which males provide very little care (e.g. Gowaty, 1983) to those in which male care is essential, such as in most seabirds (e.g. Chaurand and Weimerskirch, 1994). Even in systems in which males and females share parental care, conflict can arise with regard to the level of sex-specific parental care (Barta *et al.*, 2002). Sex-specific reproductive investment can arise for a variety of reasons, among which are differences in extra-pair mating behaviour (e.g. Trivers, 1972; Mauck *et al.*, 1999; Houston *et al.*, 2005) and sexual differences in size and foraging ability (Lewis *et al.*, 2005).

Differences in foraging and provisioning behaviour between the sexes have been well studied in monogamous seabirds (for a review, see Lewis *et al.*, 2002), where both sexes often perform similar tasks during both the incubation and chick provisioning phases of reproduction. Whereas some studies have revealed no detectable sex-specific differences in reproductive effort (e.g. Hedd *et al.*, 2002; Gladbach *et al.*, 2009), both female-biased effort (e.g. Creelman and Storey, 1991) and male-biased effort (e.g. Gray and Hamer, 2001) have been demonstrated in a growing number of seabird species. In general, however, much of this variation in effort can be attributed to size dimorphism, with the larger sex contributing more to parental care due to its greater capacity to bear the costs (Gonzalez-Solis *et al.*, 2000). Only recently has attention been paid to species with little or no size dimorphism. These studies have focused on foraging behaviour and food delivery and have shown both female-biased (Thaxter *et al.*, 2009) and male-biased (Lewis *et al.*, 2002) parental care.

Leach's storm-petrel (*Oceanodroma leucorhoa*), a member of the avian order Procellariiformes, is a long-lived seabird with negligible size dimorphism (Huntington *et al.*, 1996). Unlike species in which females leave care to the males either early [e.g. some shorebirds (Székely *et al.*, 2007)] or late [e.g. some alcids (Paredes *et al.*, 2006)] in the process, procellariiform adults of both sexes invest in offspring from the day the egg is layed to offspring independence (Warham, 1990). As with all procellariiform birds, storm-petrel life history is characterized by long-term pair bonds, single-egg clutches, and extended periods of obligate biparental care. Storm-petrel pairs nest in underground burrows and produce a single egg per season. Over the span of the approximately 45-day incubation period, males and females alternate individual incubation bouts (subunits of the incubation period when one adult remains alone on the egg for 1–7 days) during which the incubating parent fasts while its mate forages at sea (Huntington *et al.*, 1996). This may be the most energetically demanding phase of reproduction for seabirds (Chastel *et al.*, 1995; Barbraud and Chastel, 1999; Barbraud *et al.*, 1999) and an incubating adult storm-petrel loses 4–7% of its body mass per day (Ricklefs *et al.*, 1986). Once hatched, the chick is brooded for approximately 6 days, then left alone in the burrow and fed during brief, uncoordinated night-time visits (Ricklefs *et al.*, 1985) until fledging approximately

65 days later (Mauck and Ricklefs, 2005). The fact that both sexes perform the same behaviours during both incubation and chick rearing eliminates the need for a researcher to reconcile costs due to differing parental roles and thus simplifies the task of comparing parental effort across the sexes.

Equal division of care might be expected in mating systems with true monogamy and obligate biparental care (Parker, 1985), as is the case with procellariiforms generally, and Leach's storm-petrels in particular (Mauck *et al.*, 1995). It is therefore possible that no differences are detectable between males and females, or that the sexes may differ in specific instances but reveal no general pattern, i.e. that multiple sex-biased differences are distributed equally between the sexes (Wiggins and Morris, 1987). Alternatively, if the general female-biased reproductive effort proposed by Trivers (1972) for species with internal fertilization holds, then we would expect our measures to reveal female-biased reproductive effort. Male-biased reproductive effort might be expected if the initial cost of egg production renders females less able than males to invest in parental care (Carey, 1996). In the case of storm-petrels, females produce an egg that approaches 25% of adult body mass and begin incubation with depleted energy reserves (Warham, 1990). If a threshold level of parental care is required to prevent complete failure, it may be that males are selected to compensate for any reduced female effort (Barta *et al.*, 2002; Harrison *et al.*, 2009). The nutritional imbalance between the sexes should be most acute at the onset of incubation, but may persist to a lesser degree throughout the period of parental care. If so, then the pattern of male-biased effort seen in some specific aspects of seabird reproductive biology (e.g. Gray and Hamer, 2001) may be an indicator of more general male-biased care in such systems and should be detectable across multiple levels of investigation.

We investigated sex-specific reproductive effort in Leach's storm-petrel during both the incubation and chick-rearing phases of reproduction. Using a wide range of measures, we assessed both parental care and the effect of such care on parental condition. To our knowledge, this study is the first to bring such a varied combination of methods to examine sex-specific reproductive effort in a monomorphic species with obligate biparental care throughout the reproductive cycle.

## METHODS

### Study population

We carried out this study from June through October, in the years 1991–1993, 2004, 2006, and 2007 at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35′N, 66°45′W). Our study population was a breeding sub-colony of approximately 500 actively nesting Leach's storm-petrel pairs. Each year, the study population is censused as part of a long-term demographic study. For this study, we sampled different subsets of burrows in each year. All individuals in the study population were fitted with a unique USFWS band for identification.

### Behavioural monitoring – nest attendance

We used passive integrated transponder (PIT) tags (Biomark, Inc.) to monitor night-time movement into and out of burrows by storm-petrel adults (Zangmeister *et al.*, 2009) during the incubation and chick-rearing periods. Breeding adults were captured by hand in the underground burrow. The PIT tags were attached to birds with plastic leg bands, and antennas were placed around the burrow entrances to detect the PIT tags. When a tagged bird passed through an antenna, the date, time, and identification number unique to that tag were recorded.

We monitored nest attendance during incubation using PIT tag technology (Zangmeister *et al.*, 2009) in seven burrows during the 2006 season. Burrows were chosen arbitrarily for their proximity to the power source needed to power the PIT monitors. Three of the seven eggs did not hatch, but because PIT tag data showed that adults in at least two of these burrows continued to attend the egg well beyond the normal incubation period (~42 days; C.E.H.), they were included in the behaviour analyses since extended incubation of infertile eggs is well known in storm-petrels (Boersma *et al.*, 1980). Nest attendance during the incubation period was monitored for an additional eight nests in 1993 (see next sub-section).

We also used PIT technology to monitor nest attendance during the chick-rearing period. During the 2004 season, we monitored nest attendance in three burrows during chick growth from 28 August to 27 September. In 2006, we monitored the four PIT-tagged pairs whose eggs had hatched successfully from 15 July to 28 September. We monitored an additional three burrows in 2007 from 28 July to 28 September. All ten burrows were occupied by different pairs of breeding storm-petrels. The chicks in these burrows were weighed daily between 09.00 and 11.00 h. Chick mass was recorded to the nearest 0.1 g using an OHAUS 100 electronic balance. Storm-petrel parents provisioning chicks remain in the burrow anywhere from a few minutes to a few hours before departing the same night. The PIT technology allowed us to assess whether a single adult, both adults, or no adults attended the nest the previous night and match that event with the 24-h change in mass of the chick.

### Behavioural monitoring – incubation tenacity

Storm-petrels with infertile eggs will extend incubation up to 20 days past the expected hatch date (Wheelwright and Boersma, 1979; Huntington *et al.*, 1996). We term such an extension ‘incubation tenacity’, an index of the willingness of an individual storm-petrel to continue incubation behaviour even when an egg does not hatch. We tested sex-specific patterns of incubation tenacity with eight randomly chosen breeding pairs of petrels in 1992 and eight different pairs in 1993. We monitored each burrow daily for the appearance of the egg. When an egg appeared, we removed the incubating adult from the burrow by hand, recorded its USFWS band number, and fitted it with a PIT tag. When the other member of the pair replaced its mate in the burrow, we repeated the procedure for the second bird. From that point forward, we used a hand-held PIT scanner to determine daily the identity of incubating adults with minimal disturbance. The first time an egg was left unattended (egg neglect) 20 days or more after being laid, it was replaced in the burrow by a dummy egg of similar size and weight. We continued to record the identity of the incubating parent in each burrow until incubation was abandoned. We defined abandonment as seven or more days of continuous neglect. In 1992, we investigated only incubation tenacity, whereas in 1993 we also recorded total number of incubation bouts and length of incubation bouts for each adult.

### Ptilochronology

To track nutritional condition, we used ptilochronology (Grubb, 1989), a technique for gauging a bird's nutritional status by measuring growth rates of feathers. The method involves pulling a bird's rectrix (tail feather), thereby inducing a new feather to grow in its place. When the bird is recaptured more than a month later, the growth characteristics of the replacement (or induced) rectrix provide an index of the bird's nutritional status during the intervening period. A bird in good nutritional condition will grow its induced feather at a faster rate than will a bird in poorer nutritional condition (Grubb *et al.*, 1991; Grubb, 2006). We defined feather growth rate ($\text{mm} \cdot \text{day}^{-1}$) as the length (mm) of the induced rectrix (IR6) divided by the number of days since the original feather (IR6) was pulled.

To track nutritional condition during the incubation phase, we pulled the original outer right retrix (OR6) from both members of breeding pairs on approximately day 13 of incubation during the 2006 breeding season. We recaptured adults approximately 25 days after the OR6 was taken and pulled the induced rectrix (IR6) that had grown in its place. We were able to obtain both the original and induced feather from 87 breeding adults during the incubation period.

To track nutritional condition during the chick-rearing phase, we induced feather growth among adults ≤4 days post-hatch during the 1991 and 1992 breeding seasons. We recaptured adults approximately 45 days later and collected the IR6. We were able to obtain both the original and induced feathers from 123 breeding adults in 1991 ($n = 90$) and 1992 ($n = 33$).

### Bactericidal assay

In 2006, we measured innate constitutive immune function using the bactericidal assay described by Tieleman *et al.* (2005). We took blood from 124 adults by puncture of the brachial vein during the third quartile (approximately day 33) of the incubation period. Blood was taken on the first day of an individual incubation bout. We combined whole blood with *Escherichia coli* according to Tieleman *et al.* (2005) and compared the number of colonies formed on the treatment plates with a control plate (*E. coli* not exposed to blood) to assess bacteria-killing ability. Immune score was calculated as 1 – (number of *E. coli* colonies after exposure to whole blood)/(number of control colonies).

### Sexing

Adult Leach's storm-petrels are monomorphic with regard to plumage and, although female wing length is about 1% greater than male wing length, sex cannot be reliably determined morphometrically (R.A. Mauck, unpublished). Not all individuals in the colony have been identified for sex. Sexing of adults in this study during the 1992 and 1993 seasons was based on cloacal distention after Huntington *et al.* (1996). In 2006, we determined the sex of the adults in this study using the molecular technique described by Griffiths *et al.* (1998) with the exception of DNA extraction, for which we followed Tomasulo *et al.* (2002). We used PCR to amplify the chromo-helicase-DNA-binding (CHD) gene (Griffiths *et al.*, 1998) and ran the products on a 3% agarose-1000 (Invitrogen) gel at 90 V for 3.5 h. The gels were visualized with ethidium bromide staining under ultraviolet light.

### Statistics

For analyses of incubation and chick-rearing behaviour derived from PIT tag data, we used appropriate non-parametric tests when data did not meet the assumptions of parametric tests. When data were available for both members of a breeding pair, we used paired tests to assess differences between males and females. We were not able to measure both feather growth and immune function for all adults, resulting in somewhat different subsets of the population measured in each analysis. Descriptive statistics are reported as means ± standard deviations unless otherwise indicated. Statistical significance was set to $P < 0.05$. All tests were two-sided.

## RESULTS

### Study population demographics

Colony-wide hatching success in all years was similar to historical values [76.9 ± 6.4% (authors' unpublished data)], although 1991 (68.9%) and 2006 (65%) were in the lower quartile of historical records. However, colony-wide fledging success in 1991, 1992, 2004, 2006, and 2007 all exceeded 90%, values similar to those reported by Huntington *et al.* (1996). Fledging success was not monitored in 1993. Chick growth as indexed by maximum chick mass [MCM = 81.9 ± 7.3 g (after Mauck and Ricklefs, 2005)] was similar to historical means [82.2 ± 7.0 g S.E. (R.A. Mauck, unpublished)]. Colony-wide chick growth (including chicks not monitored for this study) did not differ between years included in this study [$F_{9,286} = 1.52$, $P = 0.18$ (authors' unpublished data)]. Only chicks in 1992 (MCM = 77.9 ± 11.7 g) fell outside the inter-quartile range of historical records and both 1991 (81.8 ± 2.0 g S.E.) and 2006 (81.0 ± 9.0 g S.E.) chicks were very close to historical means. Body condition (mass/wing length) for adults captured on the first day of incubation in 2004, 2006, and 2007 was similar to historical values [0.32 + 0.02 g/mm (R.A. Mauck, unpublished)] for both males (0.32 + 0.02 g/mm, $n = 67$) and females (0.32 + 0.03 g/mm, $n = 71$).

### Behaviour

#### *Incubation*

Male storm-petrels spent a greater proportion of time incubating (paired *t*-test: $t_{13} = 4.95$, $P = 0.0002$) than did females. Males remained on the eggs for 55.8 ± 4.6% of all days in which the egg was incubated. The difference was due to longer incubation bouts (paired *t*-test: $t_{13} = 3.51$, $P = 0.004$) for males (3.4 ± 0.5 days) than for females (2.9 ± 0.7 days) and male bout length exceeded female bout length in 13 of 14 monitored burrows. The average number of incubation bouts per parent did not differ (paired *t*-test: $t_{13} = 1.10$, $P = 0.29$) between pairs of males (6.9 ± 1.6 bouts) and females (6.6 ± 2.0 bouts).

Males showed greater incubation tenacity than did females. When incubating a replacement egg, males abandoned later than females in 13 of 16 nests (6 of 8 in 1993 and 7 of 8 in 1992), which is significantly different from predictions assuming equal probabilities of abandonment ($\chi^2_1 = 6.25$, $P = 0.01$).

### Chick provisioning

In nine of the ten PIT-tagged burrows that were monitored during the chick-rearing period (2004, 2006, 2007), males returned to the burrow to feed chicks more often than females ($\chi_1^2 = 6.40$, $P = 0.01$). Males were the only parent to return to the burrow on 34.8 ± 8.6% of nights the chick was in the burrow, whereas females were the only parent to attend a burrow on 11.5 ± 8.6% of nights. Both parents returned to the burrow on 25.1 ± 8.8% of nights, and on 29.3 ± 17.1% nights neither returned. Combining single-parent and both-parent nights, males made a higher percentage of food deliveries (62.3 ± 7.6%) than did females (37.7 ± 7.6%).

We modelled 24-h change in chick mass as a function of the parental attendance (male only, female only, both, none). We included chick mass, chick age, and the interaction term in the model to account for the size-specific loss of mass over the 24-h period, since size of the chick influences rate of mass loss (Ricklefs *et al.*, 1985). We included year in the full model to account for between-year differences and we included burrow (chick ID) as a random factor to account for repeated measures for each burrow ($n = 10$). In this model ($R^2 = 0.58$), only attending parent(s) had an effect on 24-h change in mass ($F_{3,363} = 121.1$, $P < 0.001$), primarily due to the significant difference ($P < 0.001$) in 24-h change in mass between nights when both parents arrived (4.79 ± 1.52 g) and when neither parent arrived (−6.03 ± 1.27 g). There was no difference ($P = 0.27$) between the adjusted mean 24-h change in mass when only the attending male delivered food (−0.32 ± 1.20 g) and only the attending female delivered food (0.27 ± 1.49 g). Single-parent nights were different from nights with both parents ($P < 0.01$) and nights with no parents ($P < 0.01$). To estimate average food delivered by each sex, we added the adjusted mean 24-h loss of mass when no parents fed the chick (−6.03 g) to the adjusted means for each sex. Estimated mean meal delivered, therefore, was similar for both males (5.7 ± 1.24 g) and females (6.4 ± 1.38 g). Estimated food delivered when both parents arrived was 10.82 g.

We calculated per-day food delivery for each sex as:

$$TotalFood_{sex} = \frac{(D_{sex} * L_{sex}) + (D_{both} * L_{both} * PL_{sex})}{d}$$

where $D_{sex}$ = number of deliveries by the focal sex, $L_{sex}$ = sex-specific load size calculated from single-sex trips, $D_{both}$ = number of deliveries by both parents, $L_{both}$ = estimated food delivered on nights when both parents arrived, $PL_{sex}$ = sex-specific portion of $L_{both}$ [i.e. $PL_M = (L_M/L_M + L_F)$, $PL_F = (L_F/L_M + L_F)$], and $d$ = total days monitored with PIT reader (includes nights with no food delivered).

Estimated mean daily food delivery by males (3.4 ± 0.4 g) was greater than estimated mean daily food delivery by females (2.2 ± 0.2 g) (paired *t*-test: $t_9 = 4.10$, $P = 0.003$).

## Ptilochronology

We constructed a model of feather growth ($\text{mm} \cdot \text{day}^{-1}$) against sex, year, and the interaction of sex and year. The full model ($F_{5,187} = 16.95$, $P < 0.001$) showed a significant effect of year ($P < 0.001$), a significant effect of sex ($P = 0.05$), and no effect of the interaction ($P = 0.8$). Adjusted mean feather growth of females ($1.64 \pm 0.09\ \text{mm} \cdot \text{day}^{-1}$) was approximately 11% greater than feather growth of males ($1.53 \pm 0.25\ \text{mm} \cdot \text{day}^{-1}$) across years.

For 80 pairs of adult petrels (1991, $n = 30$; 1992, $n = 9$; 2006, $n = 41$), we obtained feather growth values for both members of the breeding pair. To further examine the effect of sex on feather growth while controlling for nest-specific influences, we used paired tests to examine within-pair differences between the sexes. During incubation (2006), mean difference of feather growth within pairs (female – male) was $0.11 \pm 0.63$ mm · day$^{-1}$ (Wilcoxon signed rank test: $W_{40} = 62.5$, $P = 0.42$). During chick rearing (1991, 1992), mean difference between feather growth within pairs was $0.14 \pm 0.38$ mm · day$^{-1}$ (Wilcoxon signed rank test: $W_{38} = 191.0$, $P = 0.006$).

### Immune function

The average immune score for 124 individuals of known and unknown sex was $0.06 \pm 0.02$, and there was no significant difference ($t_{113} = 0.92$, $P = 0.36$) between males ($0.04 \pm 0.03$, $n = 57$) and females ($0.08 \pm 0.03$, $n = 58$), even when compared within pairs (paired *t*-test: $t_{25} = 0.62$, $P = 0.54$).

### Immune function and length of incubation bouts

To better understand sex differences with regard to incubation behaviour, we examined the relationship between immune function and length of incubation bouts. In the four burrows in 2006 for which we have immune function measures and detailed incubation behavioural data, a GLM of bout length as a function of sex, immune score, and the interaction (sex*immune score) revealed a significant effect of sex ($t = 2.92$, $P = 0.04$) and the interaction term ($t = 2.98$, $P = 0.04$). Further investigation of the significant interaction revealed that, even with such a limited sample size, immune score in males increased with average length of incubation bout (Pearson's $r = 0.97$, $P = 0.03$), and a non-significant negative effect in females (Pearson's $r = -0.72$, $P = 0.27$), perhaps due to the low sample size (power to detect a difference: 0.14).

### *Post-hoc* multiple comparisons

A conservative approach is to apply a Bonferroni correction (0.05/6 tests = 0.008) to each of the independent tests presented here. For example, since proportion of time incubated is a function of mean bout length and number of bouts, we did not use mean bout length and number of bouts in the comparison. In this way, we identified six independent tests (Table 1). Thus, under Bonferroni correction, male effort exceeds female effort during incubation in terms of proportion of time incubated and during the chick-rearing period in terms of mean daily food delivery and rate at which adults replace lost feathers (Table 1).

However, given the number and variety of tests with which we were able to examine sex-specific reproductive effort in this species and the fact that every one of these tests shows some degree of male bias (Table 1), we used Fisher's method for multiple comparisons (Fisher, 1948) to assess the probability that such a one-sided pattern for male-biased reproductive success would occur by chance alone. We used only independent tests in this comparison. Fisher's test statistic is calculated as:

$$\chi^2_{2k} = -2 \sum_{i=1}^{k} \log_e(p_i)$$

**Table 1.** Tests of sex-specific reproductive effort

| Level | Phase | Years | Test | *P*-value | Comment |
|---|---|---|---|---|---|
| Behaviour | Incubation | 1993, 2006 | **Proportion of time incubated** | **0.0002** | **M > F** ** |
| | | | Mean length of incubation bout | 0.004 | M > F * |
| | | | Number of incubation bouts | 0.29 | M > F |
| | | 1992–1993 | **Incubation tenacity** | **0.01** | **M > F** * |
| | Chick provisioning | 2004, 2006, 2007 | **Mean daily food delivery** | **0.003** | **M > F** ** |
| | | | Number of feeding trips | 0.01 | M > F * |
| | | | Load size | 0.27 | F > M |
| Physiological | Incubation | 2006 | **Feather growth** | **0.25** | **M < F** |
| | | | **Immune function** | **0.36** | **M < F** |
| | Chick provisioning | 1991–1992 | **Feather growth** | **0.006** | **M < F** ** |

*Note*: For tests of behaviour, the greater mean value is indicative of greater reproductive effort. For tests of physiology/condition, the lesser mean value is indicative of greater reproductive effort. **Bold** tests are considered independent tests under Bonferroni correction and Fisher's combined probability test. *Significant at $P < 0.05$. **Significant under Bonferroni correction (0.05/6). Every bold test trends towards male-biased effort (6 of 6) under Fisher's combined probability test ($P = 0.0008$). M = male, F = female.

where $k$ = number of tests under consideration and $p$ = the $P$-value of each of those tests. The resulting chi-squared statistic has degrees of freedom equal to $2k$.

Thus, across all tests presented here (Table 1), it is extremely unlikely that the apparent male-biased effort was due to chance alone ($\chi^2_{12} = 44.7$, $P = 0.0008$).

## DISCUSSION

Both during incubation and chick rearing, our measures of reproductive effort consistently suggest male-biased investment in this species. While other seabirds have shown sex-specific reproductive behaviour, much of it can be attributed to the size dimorphism of these species (Gonzalez-Solis, 2004; Lewis *et al.*, 2005; Navarro *et al.*, 2009) or occurs in systems such as the Alcidae in which the duration of male care exceeds that of female care (e.g. Harding *et al.*, 2004; Paredes *et al.*, 2006). Among monomorphic seabird species in which the duration of parental care is equal between the sexes, evidence for sex-specific reproductive effort has primarily been from studies of foraging behaviour (Gray and Hamer, 2001; Lewis *et al.*, 2002). It would not have been surprising either had our measures of sex-specific effort been equally distributed between the sexes (Wiggins and Morris, 1987). It is therefore striking that in multiple tests, across both incubation and chick rearing, both behavioural and physiological, our results show such one-sided evidence for male-biased investment in parental care in this long-lived, monomorphic seabird with obligate biparental care.

Males in our study invested more in incubation than did females as indexed by their behaviour. Adults incubating eggs can lose 4–7% of their body weight per day (Ricklefs *et al.*, 1986). Petrels arrive on the egg after foraging at sea with energy stored both as fat and as lipids in their proventriculus (Roby *et al.*, 1997). Thus the ability to fast is a function of stored energy and the degree to which individuals will reduce their own body condition in the face of an energy deficit. The longer incubation bouts performed by males suggest that males were more willing or able to reduce their own energy reserves between foraging trips than were females. An alternative explanation would be that females returned to the egg with fewer reserves than did males; however, we found no evidence for this in terms of adult body condition on the first day of incubation. One caveat, however, is that storm-petrels return to the burrow with varying volumes of stomach oil stored in their proventriculus (Ricklefs *et al.*, 1986). Thus, traditional measures of body condition do not reflect energy stored as fat or the current state of other necessary nutrients, such as calcium (Gravel *et al.*, 1994). However, the male-biased incubation attendance in storm-petrels is a phenomenon previously reported among other Procellariiformes, such as the Laysan albatross [*Diomedea immutabilis* (Fisher, 1971)].

Equally revealing of this sex-specific difference in reproductive effort was the difference in incubation tenacity within pairs of storm-petrels faced with an egg that would not hatch. It is possible that females may have been more able than males to detect the difference between the real egg and its artificial replacement and, therefore, have been less likely to continue incubation of a dummy egg. However, since we replaced eggs early in the incubation cycle and both sexes continued to incubate well past the normal hatch date, we do not believe that our results were compromised by this experimental artefact.

Our assay of immune function examined only one facet of the immune system (Lochmiller and Deerenberg, 2000); other tests of immune function may differ between the sexes (Zuk and Stoehr, 2002). Although we found no significant sex-bias in our measure of immune function, our results did suggest that immunocompetence in males may be indicative of individual quality such that males able to fast for long durations of time also showed a greater ability to respond to pathogens. Although this result is based on a small sample size, evidence for an effect of individual quality has been found in storm-petrels (Mauck *et al.*, 2004; Blackmer *et al.*, 2005) and other long-lived seabirds, including the blue petrel (*Halobaena caerulea*), for which adult condition was positively related to reproductive performance (Chastel *et al.*, 1995).

Male-biased reproductive effort continues into the chick-rearing period. Feeding frequency and load size have been related to foraging strategy in satellite-tracked procellariiform birds (Jouventin and Weimerskirch, 1990; Weimerskirch *et al.*, 1993). As pointed out by Gladbach *et al.* (2009), meal size and frequency may offset one another and both should be taken into account when calculating measures of effort. In the case of Leach's storm-petrels, the less frequent food delivery by females is not balanced by the small increase in meal size, since the total amount of food delivered by males was greater than that by females. Long absences between feeding visits have been interpreted as foraging trips in which adults are more concerned with self-maintenance than offspring, whereas short trips represent offspring-biased foraging trips (Granadeiro *et al.*, 1998; Gray and Hamer, 2001). Apparently, female Leach's storm-petrels are less likely to sacrifice their own self-maintenance than are males.

In contrast, Gladbach *et al.* (2009) found no sex-specific differences in incubation or provisioning behaviour across an 8-year span in the closely related Wilson's storm-petrel (*Oceanites oceanicus*), with the exception of a single year in which the resources at sea were severely limiting. In this context, female investment was lower than male investment in Wilson's storm-petrels. It is possible therefore that the years included in our study were years in which resources at sea were exceptionally low. Colony-wide hatching success was low only in 1991 and 2006. However, the 2006 values were probably depressed due to the fact that we were attempting to establish exact incubation periods in the colony that year by briefly checking the nests daily for hatching, starting on day 35 of incubation. Such daily disturbance, even that late in the incubation period, probably caused higher nest failure than normal (Blackmer *et al.*, 2004). A more reliable index of annual food availability than hatching success (a binary variable) is chick growth. Specifically, maximum mass attained by nestlings (MCM) reflects total amount of food delivered to the chick (Mauck and Ricklefs, 2005). With this measure, both 1991 and 2006 were indistinguishable from historical means on Kent Island. Together with the fact that fledging success in all years of the study was similar to historical means, it is doubtful that our results were driven by years of particularly low resource availability at sea.

The behavioural evidence for male-biased effort during chick rearing is supported by the fact that the feather growth data showed that males decreased their own net energy balance while feeding chicks more than did females. It is possible that females simply have lower basic energy needs than males and therefore have more energy available to invest in offspring or feather growth. However, the basal metabolic rate of males and females is indistinguishable (Blackmer *et al.*, 2005), suggesting that this sex-specific difference in feather growth rate is a result of a greater investment by males compared with females raising chicks.

It is interesting that growth of replacement feathers was not significantly less for males than for females during the incubation period. If males and females began the incubation phase of reproduction in similar nutritional condition, this would certainly argue against male-biased investment during the incubation period. However, among procellariiform birds, females enter the incubation period with far lower energy reserves than do males, and must also replace other nutrients involved in egg production (Warham, 1990). Storm-petrel eggs are large relative to adult body mass (20–25%) and egg formation is particularly slow in the smaller procellariiform birds than in other seabirds, requiring approximately 14 days (Whittow, 2002). Besides the cost of the energy stored in the egg, females pay the additional cost of elevated basal metabolic rate over the period of egg production (Whittow, 2002). Given the energy and nutritional deficit in which females begin incubation, female feather growth should be significantly slower than male feather growth if male and female incubation effort were equal. If male effort exceeded female effort, it might not be detectable statistically. Therefore, the non-significantly faster feather growth in females is just what might be expected if male-biased reproductive effort is driven by sex-specific differences in nutritional condition at the beginning of parental care.

Barta *et al.* (2002) used game theory to study sex-specific conflict over parental care with respect to energy reserves. They showed that under some circumstances where biparental care is advantageous, females might strategically reduce their own energy reserves to induce greater investment by males. Although in their model such reductions are the product of state-dependent decisions throughout the reproductive cycle, in the case of storm-petrels, female energy reserves are depleted at the beginning of the incubation period due to the costs of egg production. In either case, if a threshold level of parental care is required to prevent complete failure, it may be that males are selected to compensate for reduced female effort from that point forward. Numerous studies have demonstrated at least partial compensation to reduced effort by one partner (Harrison *et al.*, 2009). Although the nutritional imbalance between the sexes should be most acute during incubation, the continued male-biased effort through chick provisioning may reflect a continued, though lessened, nutritional imbalance between the sexes.

It is also possible that male-biased parental effort can be explained by the importance of pair bonds to long-lived birds. Pair bond duration increases reproductive success, particularly in seabirds (Wittenberger, 1980; Thibault, 1994; Fowler, 1995; Pyle *et al.*, 2001; Wiktander *et al.*, 2001; Bried *et al.*, 2003). It therefore may be that male reproductive effort in any one year also has a payoff in terms of future reproductive opportunities with the same partner. If females choose mates based on demonstrated male parenting ability (McNamara and Forslund, 1996), then male storm-petrels that provide a high degree of parental care not only increase the probability of success in the current year, but also increase the probability of re-mating with the same female the following year. Such pair bond continuity has a positive feedback in that it increases the probability of success in subsequent breeding attempts. Thus, we suggest it is also possible that the observed male-biased reproductive effort in Leach's storm-petrels may be a product of female choice based on male parental effort.

## ACKNOWLEDGEMENTS

We thank T.C. Grubb, Jr., D. Dearborn, and two anonymous reviewers for providing valuable comments on an earlier draft of this paper. Also thanks to C. Mauck, M. Moe, E. Vaughn, S. Mauck, R. Mauck, N. Scott-Smith, B. Lake, and A. Forbes for help with fieldwork. This research was supported by the Kenyon College Summer Science Scholars Program, the Bowdoin Scientific Station (from which this is contribution number 220), and a grant to R.A.M. and M.F.H. from the National Science Foundation (#0516784).

## REFERENCES

Ardia, D.R. 2005. Tree swallows trade off immune function and reproductive effort differently across their range. *Ecology*, **86**: 2040–2046.

Barbraud, C. and Chastel, O. 1999. Early body condition and hatching success in the snow petrel *Pagodroma nivea. Polar Biol.*, **21**: 1–4.

Barbraud, C., Weimerskirch, H., Robertson, G.G. and Jouventin, P. 1999. Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). *J. Anim. Ecol.*, **68**: 1179–1192.

Barta, Z., Houston, A., McNamara, J. and Szekely, T. 2002. Sexual conflict about parental care: the role of reserves. *Am. Nat.*, **159**: 687–705.

Blackmer, A.L., Ackerman, J.T. and Nevitt, G. A. 2004. Effects of investigator disturbance on hatching success and nest-site fidelity in a long-lived seabird, Leach's storm-petrel. *Biol. Conserv.*, **116**: 141–148.

Blackmer, A.L., Mauck, R.A., Ackerman, J.T., Huntington, C.E., Nevitt, G.A. and Williams, J.B. 2005. Exploring individual quality: basal metabolic rate and reproductive performance in storm-petrels. *Behav. Ecol.*, **16**: 906–913.

Boersma, P.D., Wheelwright, N.T., Nerini, M.K. and Wheelwright, E.S. 1980. The breeding biology of the fork-tailed storm-petrel (*Oceanodroma furcata*). *Auk*, **97**: 268–282.

Bried, J., Pontier, D. and Jouventin, P. 2003. Mate fidelity in monogamous birds: a re-examination of the Procellariiformes. *Anim. Behav.*, **65**: 235–246.

Carey, C. 1996. Female reproductive energetics. In *Avian Energetics and Nutritional Ecology* (C. Carey, ed.), pp. 324–374. New York: Chapman & Hall.

Chastel, O., Weimerskirch, H. and Jouventin, P. 1995. Body condition and seabird reproductive-performance – a study of three petrel species. *Ecology*, **76**: 2240–2246.

Chaurand, T. and Weimerskirch, H. 1994. The regular alternation of short and long foraging trips in the Blue Petrel *Halobaena caerulea* – a previously undescribed strategy of food provisioning in a pelagic seabird. *J. Anim. Ecol.*, **63**: 275–282.

Creelman, E. and Storey, A.E. 1991. Sex differences in reproductive behavior of Atlantic puffins. *Condor*, **93**: 390–398.

Fisher, H. 1971. The Laysan Albatross: its incubation, hatching and associated behaviors. *Living Bird*, **10**: 19–78.

Fisher, R.A. 1948. Combining independent tests of significance. *Am. Stat.*, **2**: 30.

Fowler, G.S. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. *Integr. Comp. Biol.*, **35**: 318–328.

Ghalambor, C.K. and Martin, T.E. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Anim. Behav.*, **60**: 263–267.

Ghalambor, C.K. and Martin, T.E. 2001. Fecundity–survival trade-offs and parental risk-taking in birds. *Science*, **292**: 494–497.

Gladbach, A., Braun, C., Nordt, A., Peter, H. and Quillfeldt, P. 2009. Chick provisioning and nest attendance of male and female Wilson's storm petrels *Oceanites oceanicus. Polar Biol.*, **32**: 1315–1321.

Gonzalez-Solis, J. 2004. Sexual size dimorphism in northern giant petrels: ecological correlates and scaling. *Oikos*, **105**: 247–254.

Gonzalez-Solis, J., Croxall, J.P. and Wood, A.G. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos*, **90**: 390–398.

Gowaty, P.A. 1983. Male parental care and apparent monogamy among Eastern Bluebirds (*Sialia sialis*). *Am. Nat.*, **121**: 149–157.

Granadeiro, J.P., Nunes, M., Silva, M.C. and Furness, R.W. 1998. Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Anim. Behav.*, **56**: 1169–1176.

Gravel, J., Van der Wal, R., Van Balen, J.H. and Van Noordwijk, A.J. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature*, **368**: 446–448.

Gray, C.M. and Hamer, K.C. 2001. Food-provisioning behaviour of male and female Manx shearwaters, *Puffinus puffinus. Anim. Behav.*, **62**: 117–121.

Griffiths, R., Double, M.C., Orr, K. and Dawson, R.J.G. 1998. A DNA test to sex most birds. *Molec. Ecol.*, **7**: 1071–1075.

Grubb, T.C., Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *Auk*, **106**: 314–320.

Grubb, T.C., Jr. 2006. *Ptilochronology: Feather Time and the Biology of Birds*. New York: Oxford University Press.

Grubb, T., Jr., Waite, T.A., Wiseman, A.J. 1991. Ptilochronology: induced feather growth in northern cardinals varies with age, sex ambient temperature, and day length. *Wilson Bull.*, **103**: 435–445.

Harding, A.M.A., Van Pelt, T.I., Lifjeld, J.T. and Mehlum, F. 2004. Sex differences in little auk (*Alle alle*) parental care: transition from biparental to paternal-only care. *Ibis*, **146**: 642–651.

Harrison, F., Barta, Z., Cuthill, I. and Szekely, T. 2009. How is sexual conflict over parental care resolved? A meta-analysis. *J. Evol. Biol.*, **22**: 1800–1812.

Hedd, A., Gales, R. and Brothers, N. 2002. Provisioning and growth rates of Shy Albatrosses at Albatross Island, Tasmania. *Condor*, **104**: 12–29.

Houston, A.I., Szekely, T. and McNamara, J.M. 2005. Conflict between parents over care. *Trends Ecol. Evol.*, **20**: 33–38.

Huntington, C.E., Butler, R.G. and Mauck, R.A. 1996. Leach's storm-petrel (*Oceanodroma leucorhoa*). In *Birds of North America*, No. 233 (A. Poole and F. Gill, eds.). Philadelphia, PA: Academy of Natural Sciences/Washington, DC: American Ornithologists Union.

Jouventin, P.W. and Weimerskirch, H. 1990. Satellite tracking of wandering albatrosses. *Nature*, **343**: 746–748.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N. *et al.* 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proc. R. Soc. Lond. B*, **269**: 1687–1693.

Lewis, S., Schreiber, E.A., Daunt, F., Schenk, G.A., Orr, K., Adams, A. *et al.* 2005. Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis*, **147**: 408–414.

Lindén, M.M. and Møller, A.P. 1989. Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.*, **4**: 367–371.

Lochmiller, R.L. and Deerenberg, C. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*, **88**: 87–98.

Mauck, R.A. and Ricklefs, R.E. 2005. Control of fledging age in Leach's storm-petrel, *Oceanodroma leucorhoa*: chick development and prefledging mass loss. *Funct. Ecol.*, **19**: 73–80.

Mauck, R.A., Waite, T.A. and Parker, P.G. 1995. Monogamy in Leach's storm-petrel: DNA-fingerprinting evidence. *Auk*, **112**: 473–482.

Mauck, R.A., Marschall, E.A. and Parker, P.G. 1999. Adult survival and imperfect assessment of parentage: effects on male parenting decisions. *Am. Nat.*, **154**: 99–109.

Mauck, R.A., Huntington, C.E. and Grubb, T.C. 2004. Age-specific reproductive success: evidence for the selection hypothesis. *Evolution*, **58**: 880–885.

McNamara, J.M. and Forslund, P. 1996. Divorce rates in birds: predictions from an optimization model. *Am. Nat.*, **147**: 609–640.

Milonoff, M., Poysa, H., Runko, P. and Ruusila, V. 2004. Brood rearing costs affect future reproduction in the precocial common goldeneye *Bucephala clangula. J. Avian Biol.*, **35**: 344–351.

Monaghan, P. and Nager, R.G. 1997. Why don't birds lay more eggs? *Trends Ecol. Evol.*, **12**: 270–274.

Navarro, J., Kaliontzopoulou, A. and Gonzalez-Solis, J. 2009. Sexual dimorphism in bill morphology and feeding ecology in Cory's shearwater (*Calonectris diomedea*). *Zoology*, **112**: 128–138.

Paredes, R., Jones, I.L. and Boness, D.J. 2005. Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Anim. Behav.*, **69**: 197–208.

Paredes, R., Jones, I.L. and Boness, D.J. 2006. Parental roles of male and female thick-billed murres and razorbills at the Gannet Islands, Labrador. *Behaviour*, **143**: 451–481.

Parker, G.A. 1985. Models of parent–offspring conflict 5. Effects of the behavior of the two parents. *Anim. Behav.*, **33**: 519–533.

Pyle, P., Sydeman, W.J. and Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *J. Anim. Ecol.*, **70**: 1088–1097.

Ricklefs, R.E., Day, C.H., Huntington, C.E. and Williams, J.B. 1985. Variability in feeding rate and meal size of Leach's storm-petrel at Kent Island, New Brunswick. *J. Anim. Ecol.*, **54**: 883–898.

Ricklefs, R.E., Roby, D.D. and Williams, J.B. 1986. Daily energy expenditure by adult Leach's storm-petrels during the nesting cycle. *Physiol. Zool.*, **59**: 649–660.

Roby, D.D., Taylor, J.R.E. and Place, A.R. 1997. Significance of stomach oil for reproduction in seabirds: an interspecies cross-fostering experiment. *Auk*, **114**: 725–736.

Székely, T., Kosztolányi, A., Küpper, C. and Thomas, G. 2007. Sexual conflict over parental care: a case study of shorebirds. *J. Ornithol.*, **148**: 211–217.

Thaxter, C.B., Daunt, F., Hamer, K.C., Watanuki, Y., Harris, M.P., Gremillet, D. *et al.* 2009. Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? *J. Avian Biol.*, **40**: 75–84.

Thibault, J.C. 1994. Nest-site tenacity and mate fidelity in relation to breeding success in Cory's shearwater *Calonectris diomedea. Bird Stud.*, **41**: 25–28.

Tieleman, B.I., Williams, J.B., Ricklefs, R.E. and Klasing, K.C. 2005. Constitutive innate immunity is a component of the pace-of-life syndrome in tropical birds. *Proc. R. Soc. Lond. B*, **272**: 1715–1720.

Tomasulo, A.M., Del Lama, S.N. and Rocha, C.D. 2002. Molecular method of sexing waterbirds without DNA extraction. *Waterbirds*, **25**: 245–248.

Trivers, R.L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871–1971* (B. Campbell, ed.), pp. 136–179. Chicago, IL: Aldine.

Warham, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. London: Academic Press.

Weimerskirch, H., Salamolard, M., Sarrazin, F. and Jouventin, P. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**: 325–342.

Wheelwright, N.T. and Boersma, P.D. 1979. Egg chilling and the thermal environment of the fork-tailed storm-petrel (*Oceanodroma furcata*) nest. *Physiol. Zool.*, **52**: 231–239.

Whittow, G.C. 2002. Seabird reproductive physiology and energetics. In *Biology of Marine Birds* (E.A. Schreiber and J. Burger, eds.), pp. 409–438. Boca Raton, FL: CRC Press.

Wiggins, D.A. and Morris, R.D. 1987. Parental care of the Common Tern *Sterna hirundo. Ibis*, **129**: 533–540.

Wiktander, U., Olsson, O. and Nilsson, S.G. 2001. Age and reproduction in lesser spotted woodpeckers (*Dendrocopos minor*). *Auk*, **118**: 624–635.

Williams, G.C. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.

Wittenberger, J.F.T. and Tilson, R.L. 1980. The evolution of monogamy. *Annu. Rev. Ecol. Syst.*, **11**: 197–232.

Zangmeister, J.L., Haussman, M.F., Cerchiara, J. and Mauck, R.A. 2009. Incubation success and nest attendance: combining PIT and nest-termperature data reveals individual-specific behavior in Leach's storm-petrels. *J. Field Ornithol.*, **80**: 373–379.

Zuk, M. and Stoehr, A.M. 2002. Immune defense and host life history. *Am. Nat.*, **160**: S9–S22.