

# Exploring individual quality: basal metabolic rate and reproductive performance in storm-petrels

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Despite evidence that some individuals achieve both superior reproductive performance and high survivorship, the factors underlying variation in individual quality are not well understood. The compensation and increased-intake hypotheses predict that basal metabolic rate (BMR) influences reproductive performance; if so, variation in BMR may be related to differences in individual quality. We evaluated whether BMR measured during the incubation period provides a proximate explanation for variation in individual quality by measuring the BMRs and reproductive performance of Leach's storm-petrels (*Oceanodroma leucorhoa*) breeding on Kent Island, New Brunswick, Canada, during 2000 and 2001. We statistically controlled for internal (body mass, breeding age, sex) and external (year, date, time of day) effects on BMR. We found that males with relatively low BMRs hatched their eggs earlier in the season and that their chicks' wing growth rates were faster compared to males with relatively high BMRs. Conversely, BMR was not related to egg volume, hatching date, or chick growth rate for females or to lifetime ( $\leq 23$  years) hatching success for either sex. Thus, for males but not for females, our results support the compensation hypothesis. This hypothesis predicts that animals with low BMRs will achieve better reproductive performance than animals with high BMRs because they have lower self-maintenance costs and therefore can apportion more energy to reproduction. These results provide evidence that intraspecific variation in reproductive performance is related to BMR and suggest that BMR may influence individual quality in males. *Key words*: basal metabolic rate, compensation hypothesis, individual quality, Leach's storm-petrel, *Oceanodroma leucorhoa*, reproductive performance. [*Behav Ecol* 16:906–913 (2005)]

Numerous studies have concluded that individual quality influences reproductive performance (e.g., Copley et al., 1998; Mauck et al., 2004; Thomas and Coulson, 1988). For example, some individuals consistently have better reproductive performance than others, irrespective of age or environmental conditions (e.g., Bradley et al., 2000; Copley et al., 1998; Johannesen et al., 2003). Often, these successful breeders also have long life spans, whereas poor breeders disappear from the population relatively quickly (e.g., Harris and Wanless, 1995; Mauck et al., 2004; Thomas and Coulson, 1988; Wooller et al., 1989). This positive correlation between reproductive success and survivorship defines individual quality (Curio, 1983; Forslund and Pärt, 1995).

Several experimental studies have exchanged small and large eggs among breeding pairs to separate the effects of egg size from attributes of parents raising chicks (e.g., Amundsen and Stokland, 1990; Reid and Boersma, 1990; Risch and Rohwer, 2000). These studies have concluded that individual quality of the parent has an important influence on nestling

growth rate, fledging success, and chick mass at fledging. Thus, in addition to age and breeding experience, an individual's inherent attributes influence reproductive performance.

Because energy management is related to fitness (Ricklefs and Wikelski, 2002), it is logical to look to energetic explanations for variation in individual quality. One plausible explanation for this variation lies in the differences in energy available for reproduction. Basal metabolic rate (BMR) represents the energetic cost of maintaining body tissue and vital bodily functions apart from thermoregulation and activity costs (Kleiber, 1961), primarily through mitochondrial adenosine triphosphate synthesis (Rolfe and Brown, 1997). Although BMR may be unrelated to reproductive performance, two existing hypotheses plausibly link BMR to individual quality. These hypotheses relate intraspecific variation in BMR to reproductive performance and are based on the premise that animals must partition their available energy between self-maintenance, growth, and reproduction.

The compensation hypothesis (terminology after Nilsson, 2002) predicts that an animal with a low BMR relative to its body mass (hereafter relative BMR) should achieve better reproductive performance than an animal with a high relative BMR because it has lower self-maintenance costs and therefore can apportion more energy to reproduction (also referred to as the allocation hypothesis by Gadgil and Bossert, 1970). If so, animals with low relative BMRs should be high-quality individuals. Conversely, the increased-intake hypothesis (terminology after Nilsson, 2002) predicts that an animal with a high relative BMR should achieve better reproductive

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performance than an animal with a low relative BMR. A high relative BMR typically is associated with a proportionately large intestinal system, liver, kidneys, and heart (Daan et al., 1990; Konarzewski and Diamond, 1995; Speakman and McQueenie, 1996); thus, an animal with a high relative BMR may be able to absorb and then devote more energy to reproduction than an animal with a low relative BMR (Hayes et al., 1992; McNab, 1980; Thompson, 1992). If so, animals with high relative BMRs should be high-quality individuals that achieve better reproductive performance.

The compensation and increased-intake hypotheses have been tested several times. In small mammals, studies have not revealed a relationship between female BMR (or resting metabolic rate) and reproductive parameters, such as litter size, litter mass, offspring mass, and neonate growth rate (reviewed in Johnson et al., 2001). In contrast, Nilsson (2002) found evidence for the increased-intake hypothesis in marsh tits (*Parus palustris*) by demonstrating that parental BMR increased when brood sizes were experimentally increased. Chastel et al. (2003) also demonstrated in sparrows that early breeders had higher levels of thyroid hormone in their blood than late breeders and that thyroid levels were positively correlated with BMR, which might suggest a mechanism underlying the increased-intake hypothesis.

Here, we evaluate whether variation in BMR is related to variation in reproductive success, which is one component of individual quality in birds. In particular, we examined the relationship between BMR measured during the incubation period and reproductive performance in a long-lived procellariiform, Leach's storm-petrel (*Oceanodroma leucorhoa*). Long-term data from our study site (1955–1995) demonstrate that reproductive success varies among individuals according to some inherent characteristic that is independent of age. Age-related reproductive success in these birds can largely be attributed to phenotypic differences between individuals such that there is a positive correlation between reproductive success in the initial breeding years and longevity—in other words, individual quality (Mauck et al., 2004). Thus, Leach's storm-petrels are an appropriate species to study the basis of individual quality. We employed four parameters commonly used to examine avian reproductive performance: hatching date, chick growth rate, egg volume, and lifetime hatching success.

### Indices of reproductive performance

Hatching date is a useful index of a parent's reproductive performance because offspring that hatch earlier in the season typically survive better than later hatching chicks (e.g., Blums et al., 2002; Price et al., 1988), particularly in long-lived seabirds (e.g., Catry et al., 1998; Harris, 1979; Hatch and Nettleship, 1998; Spear and Nur, 1994). Additionally, individual quality is believed to influence hatching date and other factors related to the timing of breeding in long-lived birds, with high-quality individuals breeding earlier in the season than low-quality individuals (e.g., Aebischer, 1993; Copley et al., 1998; Morbey and Ydenberg, 2000).

Chick growth rates frequently are used to measure parental reproductive performance, and seabird chicks exhibiting fast growth rates often have higher survival rates than slower growing chicks (e.g., Coulson and Porter, 1985; Nisbet et al., 1995). Furthermore, chicks of higher quality parents often grow faster than chicks of lower quality parents (e.g., Copley et al., 1998; Hipfner, 1997; Wendeln and Becker, 1999).

Egg volume influences chick survival in kittiwake gulls (*Rissa tridactyla*), lesser black-backed gulls (*Larus fuscus*), and common terns (*Sterna hirundo*) and is related to chick growth rates in roseate terns (*Sterna dougallii*; review by Williams,

1994). In addition, egg volume often is discussed in the context of individual quality. For example, Croxall et al. (1992) reported that 50% of the variation in egg volume was attributable to individual quality in wandering albatrosses (*Diomedea exulans*). Egg volume also is used as an index of individual quality in experimental studies to separate the effects of female quality from the effects of egg size per se on nestling growth rate (e.g., Amundsen and Stokland, 1990; Amundsen et al., 1996; Hipfner and Gaston, 1999), fledging success (Reid and Boersma, 1990), and chick survival (Bolton, 1991).

Although lifetime reproductive success is difficult to determine, especially in long-lived animals (Clutton-Brock, 1988; Newton, 1989), it is thought to be strongly influenced by individual quality in several long-lived birds (e.g., Copley et al., 1998; Croxall et al., 1992; Thomas and Coulson, 1988). Because natal philopatry by Leach's storm-petrels is very low (Mauck et al., 2004), we could not determine the actual number of recruited offspring produced by an adult. Therefore, we used lifetime hatching success as an index of lifetime reproductive success prior to the year in which we measured a bird's BMR.

## MATERIALS AND METHODS

### Study species

We conducted this study at Kent Island, New Brunswick, Canada (44° 35' N, 66° 45' W), during the 2000 and 2001 breeding seasons. Huntington et al. (1996) have described the breeding biology of Leach's storm-petrels in detail. Relevant here, Leach's storm-petrels are small (45 g), long-lived (>35 years) procellariiforms that nest in burrows. Each breeding season, the female lays a single egg; both parents then incubate the egg for an average of 43 days in shifts lasting from 1 to 6 days. Parents sustain themselves during incubation on energy stored as body fat and lipid-rich stomach oil in the proventriculus. In the colony, eggs hatch asynchronously during a 1- to 2-month period.

Huntington's research population allowed us to study individuals of known sex and breeding age (range: 1–23 years). We knew each bird's breeding age (i.e., the number of years it had bred) rather than its chronological age because banded chicks rarely return to the island to breed (<2%; Huntington, unpublished data). However, through systematic searches each year we locate all birds breeding for the first time within the study area (Mauck et al., 2004), and because individuals breed in the same vicinity throughout their lifetime (Huntington et al., 1996), we were likely to have located them during their initial breeding year. Data from the subset of chicks that have returned to the island indicate that Leach's storm-petrels begin breeding annually at  $5 \pm 1$  years of age (Huntington et al., 1996). Thus, breeding age and chronological age are highly correlated. We could not precisely determine the initial breeding year for nine individuals because we had located these birds first breeding in burrows that had been previously occupied by other birds but we had not visited those burrows during the preceding 1–4 years. Therefore, we estimated the breeding ages of four birds to within 1 year (i.e., we considered the birds to have been in their initial breeding year, but they may have been breeding for either the first or second time) and five birds to within 4 years by using a breeding age intermediate between the maximum and minimum possible values.

### Indices of reproductive performance

Hatching date and chick growth rates were measured in 2001 only. In most cases, egg volume and lifetime hatching success were determined for birds measured in either year of the

study. We did not include annual hatching success as an index of reproductive performance because most (77 of 95) birds in our study were successful.

We determined hatching dates in 2001 by reaching into the burrow daily to feel for the presence of an egg or chick, beginning a few days before the anticipated date of hatching (estimated by egg candling; Blackmer, personal observation, following Weller, 1956). Eight eggs hatched in early August when no investigators were present. We estimated these hatching dates by measuring the structural sizes (mm) of the chicks in mid-August and calculating the chicks' ages using preestablished methods (chick age [days] =  $-10.313 + [0.233 \times \text{flattened wing chord}] + [1.125 \times \text{short tarsus}]$ ;  $r^2 = .94$ ,  $n = 100$  chicks; Mauck, unpublished data, following Furness, 1983; Harris et al., 1992). We then subtracted the chicks' ages from the date on which their structural measurements were taken to determine the hatching dates.

We measured chick wing growth rates in 2001 during the developmental period when wing growth is linear (between 20 and 50 days of age; Mauck and Ricklefs, 2005). We measured all chicks during the same time period (18–28 August) to reduce any seasonal variation in chick growth, which has been reported in some other seabirds (e.g., Morbey and Ydenberg, 2000; Viñuela et al., 1996). We calculated chick growth rate over this 10-day period using the following equation: wing growth rate ( $\text{mm day}^{-1}$ ) = (flattened wing chord length<sub>day 10</sub> – flattened wing chord length<sub>day 0</sub>)/10 days. For three chicks, we calculated wing growth rate over a 5-day period (23–28 August) because on 18 August they were <20 days of age and therefore may not have exhibited linear wing growth rates.

We estimated egg volume for females whose BMRs we measured using the following equation: volume ( $\text{mm}^3$ ) =  $(0.512 \times \text{length} \times \text{width}^2)/1000$  (Hoyt, 1979).

We used long-term data to calculate the lifetime hatching success (the number of successful hatches divided by the number of nesting attempts) of each bird for whom we had an unambiguous record of hatching success during its entire breeding life span prior to the year in which we measured its BMR. We excluded birds for whom more than 1 year of data ( $n = 38$ ) were missing. A failure was recorded in years in which the egg did not hatch or when we located a known breeding adult in a burrow that was not associated with an egg (i.e., skipped a breeding year). Hatching success during the year that the adult's BMR was measured and years in which human disturbance caused a failure (e.g., an investigator broke the egg or caused egg desertion) were excluded from estimates of lifetime hatching success.

### Basal metabolic rate

BMR is defined as the rate of energy expenditure (measured as oxygen consumption rate,  $\text{VO}_2$ ) by an animal during its normal resting phase with no costs of thermoregulation or digestion (Kleiber, 1961). Preliminary tests on 12 adult Leach's storm-petrels that were incubating eggs (not included in any subsequent analyses) indicated that basal oxygen consumption rates occurred when (1) birds were placed in a dark, insulated respirometry chamber maintained at 28°C (i.e., within the thermoneutral zone; Ochoa-Acuña and Montevecchi, 2002); (2) birds had rested quietly in the chamber for  $\geq 1.5$  h; (3) oxygen consumption rates were measured during daylight between 1030 and 1800 h (the normal resting period during incubation; Ochoa-Acuña and Montevecchi, 2002); and (4)  $\text{VO}_2$  was measured on the second day of an individual's incubation shift. Measuring  $\text{VO}_2$  on the second day of an individual's incubation shift ensured that each bird had not fed in >24 h and thus was likely to be postabsorptive (i.e.,

metabolizing lipids stored as either stomach oils or fats) rather than digesting food. We did not sample birds that were past day 2 of incubation because this would have substantially decreased sample sizes, as petrel incubation shift length averages 2.5 days (Huntington et al., 1996).

We controlled for any potential influences of incubation stage by measuring each individual's BMR during the middle third of its 43-day incubation period. To estimate this time period, we visited each bird's burrow early in the breeding season and determined the current incubation stage by egg candling (Blackmer, personal observation, following Weller, 1956). We then visited each burrow for several days before the bird's targeted test date so that we could capture it on the second day of its incubation shift. We transported the bird in a cloth bag to a nearby laboratory (<10-min walk) and returned it to its burrow within 3–4 h. Removing the incubating parent for this period presumably did not compromise its egg's viability because parents often neglect their egg for  $\geq 1$  day at a time (Huntington et al., 1996), and no eggs were destroyed by predators.

We measured oxygen consumption rates using an open-flow respirometry system. Before each measurement, we calibrated the Sable Systems' FOX Field Oxygen Analysis System (Henderson, Nevada, USA) using dried ambient air (20.95% oxygen) drawn into the system using a Sable Systems' PP-2 pump (version 1.0). To determine BMR, we removed water vapor and carbon dioxide from air using Indicating Drierite® and soda lime, respectively, and then passed the air through a water-jacketed aluminum respirometry chamber with an airtight Plexiglas® lid. We used two chambers in 2000 so that one bird could acclimatize to laboratory conditions while we measured another birds' oxygen consumption rate. We used a single chamber in 2001. In both years, birds were held in the chamber for the same amount of time (1.5–2.5 h) prior to the measurement of oxygen consumption. The rate of incurrent air was regulated at  $620 \text{ ml min}^{-1}$  in 2000 and  $550 \text{ ml min}^{-1}$  in 2001 using mass flow controllers (Tylan® FC260 and FC2900-4S, Mykrolis Corp., Billerica, Massachusetts, USA) in conjunction with an MKS Instruments Inc. 247 Four-Channel Readout (Andover, Massachusetts, USA). Both flow meters were calibrated against a bubble meter (Levy, 1964). Moisture and carbon dioxide were removed from excurrent air using silica gel and ascarite, respectively. The oxygen analyzer monitored and averaged the oxygen content of excurrent air every 60 s and downloaded the data to a computer. Each bird's  $\text{VO}_2$  was recorded over a 30- to 60-min period. We then calculated each bird's lowest steady-state  $\text{VO}_2$  (Gessaman, 1987), in which the average rate of oxygen consumption per minute remained steady within 0.01% for 10 consecutive minutes. We calculated BMR from the oxygen consumption rate using a conversion of  $20.08 \text{ kJ l}^{-1}$  of oxygen (Schmidt-Nielsen, 1997). We weighed each bird to the nearest 0.5 g using a Pesola spring scale before and after we placed it inside the respirometry chamber, and we assumed a linear decrease in body mass when calculating the bird's body mass at the time its BMR was measured.

### Statistical analyses

We controlled for the effects of body mass, year, sex, breeding age, date within the season, and time of day on BMR by using residual BMRs calculated from a general linear model (GLM). The GLM of BMR (log transformed) included body mass (log transformed), year (2000 or 2001), breeding age, sex (male, female, or unknown), Julian date of the BMR measurement to account for seasonal effect, and time of day when the measurement was taken. Thus, an individual's residual BMR represents its metabolic rate corrected for all these potential

Table 1

Parameter estimates for GLM of log BMR as a function of log mass, year (2000, 2001), sex (male, female, unknown), breeding age (1–23 years), Julian date on which BMR was measured, and time of day when measured

Term	Estimate	SE	<i>t</i> ratio	<i>p</i> value
Log mass	0.714	0.250	2.85	.006
Year (2000)	0.021	0.008	2.54	.013
Age	−0.002	0.001	−1.49	.140
Sex (F)	0.003	0.010	0.27	.784
Sex (M)	0.005	0.010	0.47	.641
Date	0.000	0.001	0.38	.706
Time of day	0.000	0.000	0.21	.833

intrinsic (body mass, breeding age, and sex) and external (year, date, and time of day) influences on BMR.

We used Pearson's product-moment correlations to examine the relationship between residual BMR and reproductive performance for each sex. Using data from 2001, we examined the relationship of residual BMR to hatching date and chick wing growth rate. Sample sizes vary for hatching date (depending on hatching success) and for growth rate (depending on chick survival). We also examined the relationship of yearly residual BMR (measured in 2000 or 2001) to lifetime hatching success and egg volume (analyzed using females only because male BMR was not expected to influence the volume of the egg laid by the female).

We Bonferroni-corrected all alpha levels according to the number of analyses we conducted using the same data set. Therefore, for analyses of residual BMR in relation to indices of reproductive performance,  $\alpha = .05/3$  for males and  $\alpha = .05/4$  for females; elsewhere we used  $\alpha = .05$ . We log-transformed body mass and BMR data to improve homoscedasticity and linearize this relationship (Zar, 1996). Lifetime hatching success data were arcsine square root transformed to assure normality (Zar, 1996); all other variables were normally distributed. All values are presented as the mean  $\pm$  1SD.

## RESULTS

We measured the BMRs of 95 Leach's storm-petrels during the 2000 ( $n = 52$ ) and 2001 ( $n = 43$ ) breeding seasons. Sex was known for 83 birds (43 females and 40 males); however, we used all 95 individuals in the GLM to calculate residuals representing corrected log BMR values for each individual. Only log mass ( $p = .006$ , Table 1) and year ( $p = .01$ , Table 1) had significant effects on log BMR. Interaction terms were not significant. Raw BMR was greater in 2000 than in 2001 for males ( $52.6 \pm 9.7$  kJ day<sup>−1</sup> and  $46.4 \pm 7.2$  kJ day<sup>−1</sup>;  $n = 23$  and  $n = 17$ , respectively) and females ( $51.5 \pm 7.7$  kJ day<sup>−1</sup> and  $47.3 \pm 6.8$  kJ day<sup>−1</sup>;  $n = 25$  and  $n = 18$ , respectively), but there was no significant difference between the sexes ( $p > .60$ ). Body mass also was significantly higher in 2000 than in 2001 for females ( $48.3 \pm 2.7$  g and  $46.7 \pm 2.8$  g; two-sample *T*, *df* = 42,  $t = 2.40$ ,  $p = .02$ ) but not for males ( $48.4 \pm 3.1$  g and  $47.2 \pm 4.0$  g; two-sample *T*, *df* = 39,  $t = 0.99$ ,  $p = .32$ ). However, there was no effect of sex on BMR (Table 1).

BMR was related to reproductive parameters in males but not in females. We had complete, unambiguous hatching success records for 22 males, and yearly residual BMR was not related to lifetime hatching success ( $p = .65$ ,  $r = .10$ ,  $n = 22$ ; Figure 1a). However, in 2001, 14 of 17 males successfully hatched a chick. For those males, residual BMR was positively related to hatching date ( $p = .001$ ,  $r = .78$ ,  $n = 14$ ; Figure 1b)

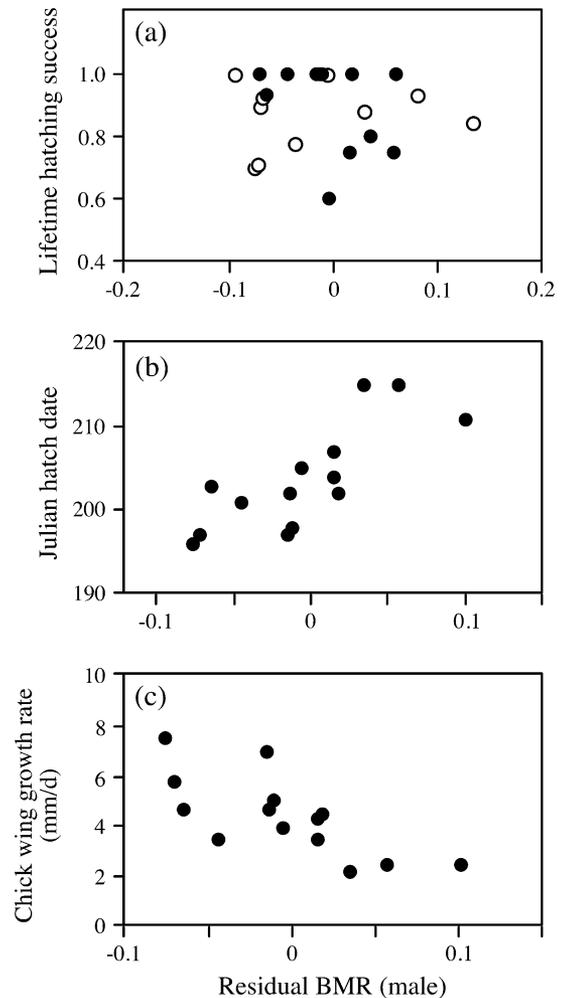


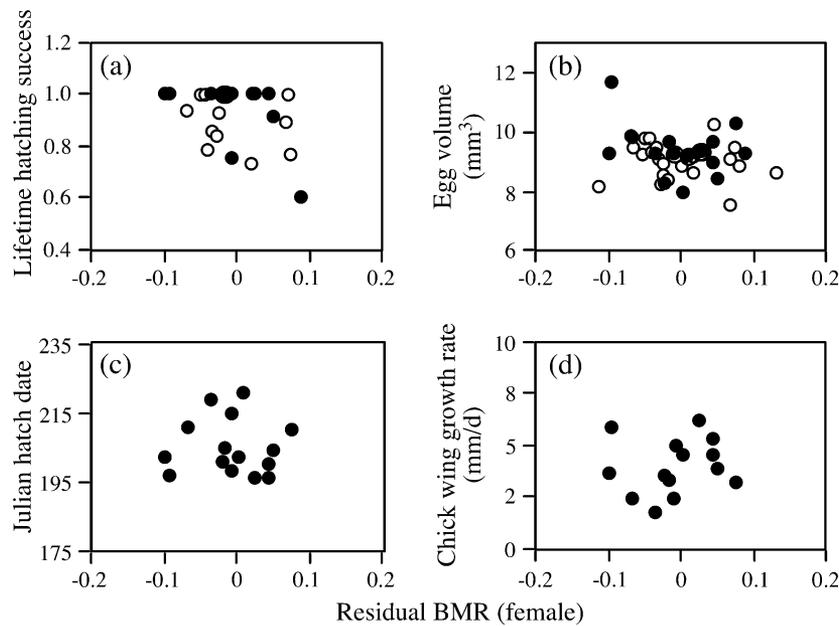
Figure 1

In male Leach's storm-petrels, the relationship between residual BMR and (a) the lifetime hatching success of males whose BMRs were measured in 2000 (open circles) or 2001 (filled circles) ( $p = .65$ ), untransformed lifetime hatching success data are presented to facilitate interpretation; (b) Julian hatching date in 2001 ( $p = .001$ ); and (c) chick wing growth rate in 2001 ( $p = .003$ ). Residual BMR was calculated using a GLM incorporating body mass, year, breeding age, sex, Julian date on which BMR was measured, and time of day when measured. BMR and body mass were log transformed to improve homoscedasticity and normality.

and negatively related to chick wing growth rate ( $p = .03$ ,  $r = -.73$ ,  $n = 14$ ; Figure 1c).

It is possible that the relationship between male BMR and hatching date was confounded by male body condition such that those individuals in better condition (with high fat reserves) began breeding earlier in the season than those in poorer condition (with low fat reserves). To address this question, we defined body condition as body mass divided by tarsus length. We then examined the relationship between the derived variable and BMR measurement date to characterize whether variation in body condition of breeding males was explained by variation in test date. Body condition was not related to measurement date for males in both years combined ( $p = .27$ ,  $r = -.18$ ,  $n = 40$ ), males in 2001 ( $p = .54$ ,  $r = -.16$ ,  $n = 17$ ), or males in 2001 that successfully produced chicks ( $p = .24$ ,  $r = -.34$ ,  $n = 14$ ).

Yearly residual BMR was not related to lifetime hatching success in females for which we had complete hatching success data ( $p = .12$ ,  $r = -.31$ ,  $n = 27$ ; Figure 2a). Residual BMR



**Figure 2**

In female Leach's storm-petrels, the relationship between residual BMR and (a) the lifetime hatching success of females whose BMRs were measured in 2000 (open circles) or 2001 (filled circles) ( $p = .12$ ), untransformed lifetime hatching success data are presented to facilitate interpretation; (b) the volume of eggs belonging to females whose BMRs were measured in 2000 (open circles) or 2001 (filled circles) ( $p = .23$ ); (c) Julian hatching date in 2001 ( $p = .91$ ); and (d) chick wing growth rate in 2001 ( $p = .58$ ). Residual BMR was calculated using a GLM incorporating body mass, year, breeding age, sex, Julian date on which BMR was measured, and time of day when measured. BMR and body mass were log transformed to improve homoscedasticity and normality.

also was not related to egg volume in females for which we measured egg volume ( $p = .23$ ,  $r = -.20$ ,  $n = 39$ ; Figure 2b); egg volume ranged from 7.6 to 10.3 mm<sup>3</sup> (mean  $9.1 \pm 0.6$  mm<sup>3</sup>). Residual BMR for females that successfully hatched a chick in 2001 also was not related to hatching date ( $p = .91$ ,  $r = -.03$ ,  $n = 15$ ; Figure 2c) or chick wing growth rate ( $p = .58$ ,  $r = .16$ ,  $n = 14$ ; Figure 2d).

## DISCUSSION

Male Leach's storm-petrels with low residual BMRs hatched their eggs earlier in the season, and their chicks' wings grew at faster rates compared to males with high residual BMRs (Figure 1b,c). These results support the compensation hypothesis (Gadgil and Bossert, 1970; Nilsson, 2002), which predicts that BMR should be negatively related to reproductive performance because individuals with low self-maintenance costs (i.e., low BMRs) can allocate more energy to reproduction than individuals with higher self-maintenance costs. Although this study did not determine how BMR and reproductive performance in petrels are related to field metabolic rate, these results provide evidence that intraspecific variation in reproductive performance is related to BMR. Conversely, we found no support for the increased-intake hypothesis in either male or female Leach's storm-petrels. BMR was not positively related to any index of reproductive performance, despite the potential for individuals with high BMRs to apportion more energy to reproduction by processing and absorbing energy more quickly than individuals with low BMRs (e.g., Daan et al., 1990; Lindström and Kvist, 1995).

It is possible that the relationship between residual BMR and hatching date in males was caused by a seasonal increase in BMR, for example, in response to changing environmental conditions (e.g., Cooper and Swanson, 1994; Williams and Tieleman, 2000). If so, males tested early in the season would have had both lower residual BMRs and earlier hatching dates

than males tested late in the season because we explicitly controlled for the physiological effects of incubation stage on BMR by measuring each individual's BMR during the middle third of its incubation period. However, we found no relationship between a male's overall BMR and the date on which his BMR was measured (Table 1). Thus, such temporal effects on BMR should not have caused the relationship between residual BMR and hatching date.

In incubating petrels, variation in body mass may be due either to structural size or to variation in the amount of body fat. It is possible that males that breed early are in better condition and carry higher fat loads than those breeding later. If so, early-breeding males may have lower residual BMRs than individuals of equal weight but with lower fat content. However, we found that males in better condition (i.e., larger mass to structural size ratio) did not breed earlier than males in poorer condition. Thus, it does not appear that body condition confounded our results.

It also is possible that if BMR declines with age (a well-documented phenomenon in mammals, including humans [Harper, 1998; Piers et al., 1998], rats [Even et al., 2001], and dogs [Harper, 1998]), then older Leach's storm-petrels could have had both lower metabolic rates and earlier hatching dates because older birds hatch their eggs earlier in the season than younger birds (Mauck, 1997). However, we statistically controlled for age-related influences on BMR when calculating residuals (Table 1), so male residual BMR should not be spuriously related to hatching date because of an effect of age on BMR. Thus, the positive relationship between male BMR and hatching date seems robust.

Because male BMR was positively related to hatching date, another spurious relationship could have occurred between male residual BMR and chick wing growth rate if early-hatched chicks' wings grew faster than those of late-hatched chicks. Slower growth rates among later hatched chicks are well documented in chin-strap penguins (*Pygoscelis antarctica*,

Viñuela et al., 1996) and alcids (e.g., Birkhead and Nettleship, 1982; Morbey and Ydenberg, 1997) and in some cases have been linked to declining food availability during the breeding season (Hedgren and Linnman, 1979; Moreno et al., 1997). However, by measuring each chick's wing growth rate during the same 10-day period in August, we minimized any seasonal effects on chick growth rates. Additionally, we controlled for the influence of chick age on wing growth rate by measuring growth rates only during the developmental period when the wing growth rate was linear (Mauck and Ricklefs, 2005). Mauck and Ricklefs (2005) also showed that chick wing growth rate is sensitive to individual variation in the timing and amount of parental input, but that growth rate is not correlated with hatching date ( $p > .45$ ; Mauck and Ricklefs, unpublished data) in Leach's storm-petrels. Therefore, the relationship between male residual BMR and chick wing growth rate also is robust.

The relationship of male residual BMR to hatching date and to chick wing growth rate suggests that BMR may provide a proximate explanation for individual quality. Many studies have concluded that inherent characteristics (i.e., independent of the effects of environmental conditions and parental age or breeding experience) influence avian reproductive success (e.g., Brouwer et al., 1995; Cogley et al., 1998; Morbey and Ydenberg, 2000). However, the underlying factors that cause individuals to vary in quality have not been identified. Because male Leach's storm-petrels with low residual BMRs had superior reproductive performance compared to males with high metabolic rates, it follows that high-quality individuals may be those that have low relative BMRs.

It is unclear why our results differed between males and females, but studies of procellariiforms have consistently demonstrated sex-related differences in reproductive effort, with males contributing more than females during the incubation and chick-rearing periods. For example, Leach's storm-petrel, Antarctic petrel (*Thalassoica antarctica*), cape petrel (*Daption capense*), giant petrel (*Macronectes* spp.), snow petrel (*Pagodroma nivea*), northern fulmar (*Fulmarus glacialis*), wandering albatross, and Laysan albatross (*Phoebastria immutabilis*) males each invest more time in incubation than their mates (Barbraud et al., 1999; Croxall and Ricketts, 1983; Fisher, 1971; Hatch, 1990; Hunter, 1984; Lorentsen and Røv, 1995; Mauck, 1997; Weidinger, 1998, respectively). Male Leach's storm-petrels also invest in the egg longer than females when their incubation period is artificially extended (i.e., females abandon the egg sooner), and males expend more effort (measured by the growth rate of replacement feathers) during the chick-rearing period than females (Mauck, 1997). Likewise, male snow petrels feed their chicks more frequently than their partners do (Barbraud et al., 1999), and the survival of wandering albatross chicks to fledging is positively correlated with the time spent incubating by males (Croxall and Ricketts, 1983). Because males undertake a larger proportion of parental care duties after the egg is laid, Hatch (1990) concluded that male quality is particularly important in breeding procellariiforms. Studies of other seabirds, particularly alcids, also have demonstrated male-biased parental care during chick rearing (e.g., Bradley et al., 2002) and the importance of male parental care to the reproductive success of a pair (e.g., Ackerman et al., 2005; Pyle et al., 2001). We suggest that high-quality males may be able to invest more time in incubation than low-quality males because having low BMRs enhances their ability to fast while their partners forage to restore their body condition after egg production. If so, these males' eggs would experience less temporary egg neglect and therefore hatch earlier in the season (Boersma and Wheelwright, 1979; Vleck and Kenagy, 1980). High-quality males with low BMRs also may be able to provision their chicks at a higher rate

than males that have greater individual energy requirements, causing their chicks to grow faster and to fledge earlier or at higher masses.

In contrast to males, a female's largest contribution to a pair's reproductive performance may occur earlier in the breeding season during egg formation. The single egg laid by a female procellariiform is unusually large for her body size (Warham, 1990). For instance, a Leach's storm-petrel egg ranges from 20% to 25% of the female's body weight (Huntington et al., 1996). Given this large investment in the egg, female quality may have a strong influence on egg volume or composition. In accordance with this hypothesis, several studies have concluded that high-quality females lay relatively large eggs (e.g., Amundsen and Stokland, 1990; Croxall et al., 1992; Wendeln, 1997; but see Amundsen, 1995) and that chicks hatched from large eggs grow faster (e.g., Amundsen and Stokland, 1990; Hipfner et al., 2001; Williams, 1980) and survive better (review by Williams, 1994) than chicks hatched from small eggs. The ability to produce large eggs probably is influenced by variation in the physiological activities involved in egg production, such as the production of yolk precursors by the liver, their uptake into ovarian follicles, and the oviduct mass (review by Christians, 2002, but see Barbraud and Chastel, 1999). Additionally, Vezina and Williams (2002, 2003) showed that BMR varies by reproductive stage. Therefore, because the size and activity of a female's reproductive organs should influence BMR, it is possible that if we had measured BMR nearer to egg laying, we may have detected an influence of female BMR on egg size.

This study addressed the relationship between BMR and reproductive performance; however, high-quality individuals are defined as those with both high survivorship and high reproductive success (Curio, 1983; Forslund and Pärt, 1995). By this definition, Leach's storm-petrels breeding at our site exhibit clear variation in individual quality because individuals with better hatching success in their first two breeding years tend to remain in the breeding population longer than birds with poor early hatching success (Mauck et al., 2004). Although we do not know yet whether BMR is related to survivorship, we have at least shown that BMR influences aspects of reproductive performance during the incubation and chick-rearing stages and provides a plausible proximate basis for individual quality in male Leach's storm-petrels.

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