

主論文

Energy and time allocation in streaked shearwater during the chick-rearing period

(育雛期におけるオオミズナギドリのエネルギーおよび時間配分)

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2016

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Chapter 1:

General Introduction

1.1. Reproductive investment strategies in long-lived animals

Sexual reproduction is one method by which the genetic materials of an organism are passed on to the next generation. Iteroparous organisms are predicted to face trade-offs with respect to how many resources to invest in their current reproduction attempt (Williams 1966), because the survival of parents is thought to be inversely related to reproductive effort (Daan et al. 1996, Golet et al. 2004). Reproductive effort is defined as the proportion of total resources that an organism devotes to reproduction (Trivers 1985). They thus have to allocate resources between these competing life history traits in order to maximize lifetime reproductive success (Stearns 1992, Zera and Harshman 2001). Important resources in this context are energy and time, and for most animals the only way to obtain energy is by expending energy while foraging.

Two main mechanisms have been proposed to explain how animals optimize the balance between current and future reproductive attempts (Nilson 2002, Navarro and González-Solís 2007). A fixed investment strategy would mean that parents employ a fixed level of investment in their current reproduction attempt to prevent depletion of their own survival. In contrast, a flexible investment strategy implies that parents can change their level of investment in their current reproduction attempt to optimize chick-rearing conditions. Generally, in long-lived animals allocation processes are predicted to prioritize self-maintenance over current reproduction, because fitness in these species primarily depends on longevity, and even a small reduction in survival will have a large negative effect on lifetime reproductive success (Charlesworth 1980).

Seabirds, which generally include all of the Procellariiformes and Sphenisciformes, all of the Suliformes except the darters, and some of the Charadriiformes (the skuas, gulls, terns, auks, and skimmers), are notable for their

extreme life history traits such as low fecundity, slow chick growth and long life expectancy (Lack 1968). These traits suggest that seabirds should prioritize self-maintenance over current reproductive output. However, several studies of seabirds have shown that reproductive effort can be flexible, and can increase in response to experimentally increased cost (e.g. Tveraa et al. 1998, Granadeiro et al. 2000, Velando and Alonso-Alvarez 2003). On the other hand, other studies show that some species accept a fixed level of investment in the current reproductive attempt (e.g. Sæther et al. 1993, Navarro and González-Solís 2007). Findings regarding the direction of energy allocation in decisions concerning their current reproductive attempt are therefore equivocal, and the mechanisms that result in these differences among studies remain unclear.

A common approach to testing these strategies in seabirds is to use an experimental manipulation of reproductive effort, such as increasing the energetic cost of flight by means of feather clipping (Bijleveld and Mullers 2009, Leclaire et al. 2011). Handicapped seabirds may change their foraging effort, adjusting their foraging trip duration to maintain their body condition (e.g. Weimerskirch et al. 1995, Duriez et al. 2000, Navarro and González-Solís 2007). As a result, either the handicapped parents or their chicks are expected to show poor body condition. However, few studies have investigated whether such manipulations sufficiently affect decisions about resource allocation by handicapped parents, or how the handicapped parents' behavioral change influences resource allocation between the parent and its chicks. In addition, theoretical approaches predict that many trade-offs appear only when breeding conditions are less favorable (Stearns 1992, Erikstad et al. 1998). Under poor breeding conditions, such as low food availability, only a small increase in reproductive effort can result in a dramatic decrease in adult survival, whereas under good breeding conditions, the

parents may increase their effort to a large extent without any drop in survival. Only beyond a certain threshold in the balance between acquired and expended energy will there be a steep increase in the risk of parental mortality as a result of increasing reproductive effort, in which case parents may be forced to choose between the two investment strategies. To better understand life history strategies in seabirds, it is therefore necessary to study how both experimental manipulation and food availability affect reproduction performance in seabirds, through their foraging behavior (Figure 1.1).

1.2 Flexible foraging strategies in seabirds

Seabirds live in a stochastic marine environment, where foraging conditions can vary widely among years (Ashmole 1971). Such variation may favor a flexible foraging strategy in which energy- and time-budgets are flexible, and which can be adjusted according to energy availability in a given breeding season (e.g. Weimerskirch 2001). Indeed, a variety of seabird species modify their foraging behavior to resolve time- and energy-constraints (e.g. Shaffer et al. 2003, Lewis et al. 2004, Welcker et al. 2009a). As a simple foraging model of energy intake and expenditure rates, under conditions of abundant energy availability, seabirds may increase their foraging effort if they can acquire energy faster than they expend it (Figure 1.2A). In this situation, adults could maximize the rate of energy delivery to offspring by increasing both their energy expenditure rate and their net rate of gain (i.e. energy intake rate minus energy expenditure rate; Ydenberg et al. 1994, Houston and McNamara 1999). In contrast, when energy availability is limited, expended energy may be reduced, in order to maximize the net rate of energy gain, which may lead to an increase in energy efficiency (i.e. energy intake per unit of energy expenditure; Figure 1.2B). In this case, individuals

may be forced to perform longer foraging trips to maintain the required level of net energy intake (i.e. net amount of energy obtained). These models predict that even when seabirds face relatively poor breeding conditions, their flexibility in energy expenditure and foraging trip duration may enable them to compensate for the negative energetic balance on their own.

A positive relationship between food availability and field metabolic rate (FMR) has been observed in some seabirds, such as black-legged kittiwakes *Rissa tridactyla* (Jodice et al. 2006) and little auks *Alle alle* (Welcker et al. 2009b), but less flexibility was observed in thick-billed murre *Uria lomvia* (Kitaysky et al. 2000), and in a second study on black-legged kittiwakes (Welcker et al. 2010). This suggests that seabirds could respond to stressors such as resource depletion using flexible time and energy allocation, but that the degree of flexibility may be different within and between species (Furness and Tasker 2000, Ronconi and Burger 2008). This self-compensation by means of a flexible foraging strategy might function as a buffer against the trade-off between self-maintenance and current reproduction success (Figure 1.1). It may therefore be important to merge aspects of foraging strategy with reproductive investment strategy to understand the decisions about energy allocation made by long-lived seabirds.

Important components of foraging flexibility (i.e. time and energy budget) in seabirds are the activities associated with energy intake and expenditure (Sibly and Calow 1986). Seabirds face morphological trade-offs between efficient travel in air and water (Birt-Friesen et al. 1989, Kovacs and Meyers 2000, Elliott et al. 2013a), and differences in morphology may be related to differences in foraging ability. Although many studies have focused on how seabirds allocate time to each activity during foraging trips (e.g. Falk et al. 2000, Ropert-Coudert et al. 2004, Paredes et al. 2012), an

often-overlooked complication is that the large differences in activity-specific metabolic rates make energy expenditure sensitive to variations in the birds' allocation of time to different activities. For instance, albatrosses, having long, narrow wings with a high aspect ratio, have large foraging ranges from their colonies (> 1000 km; e.g. Shaffer et al. 2003, Richardson 2011), which is advantageous with respect to searching for the most productive foraging grounds. On the other hand, their long wings make landings and take-offs for feeding more difficult, and increase their total energy expenditure (Weimerskirch et al. 2000b, Shaffer et al. 2001). The differences in activity-specific costs between species may strongly influence their extent of foraging flexibility in the face of changes in energy availability. It is therefore crucial to reveal the behavioral factors affecting energy intake and expenditure rates in seabird species, in order to understand the extent of foraging options associated with different levels of energy availability.

1.3. Measuring energy expenditure in free-ranging individuals

Understanding of the activity-specific metabolic rates will require knowledge of individual energy expenditure that correlates of variation in foraging behaviors. However, the measurement of individual metabolic rates (e.g. resting metabolic rate [RMR], field metabolic rate [FMR]) remain a challenge, although they also could give a valid picture of investment by an adult in a current breeding attempt (Ricklefs and Wikelski 2002).

To date, several methods have been used for measuring metabolism and energy expenditure in animals (Halsey 2011). Because each method includes both random and systematic error, they vary in accuracy (i.e. the closeness of an estimated value to its true value) and precision (i.e. the closeness of repeated measurements of the same

quantity to each other). Respirometry, which is among the most commonly used technique for measuring the baseline of energy metabolism, has been used for at least 200 years (Halsey 2011). Energy demands calculation using an open-flow respirometric system, one of the main respirometry techniques, has high precision (coefficient of variation within 3%; Sparling et al. [2008]) and accuracy (mean error within 3%; Withers [1977]). However respirometry system requires keeping the animal in a metabolic chamber and it is not possible to replicate the natural environment within such small chamber. Thus, other methods have been developed to measure metabolic rates of free-ranging animals in the wild (i.e. field metabolic rate) (Halsey 2011).

Among the methods to measure FMR, the doubly labeled water (DLW) method is considered a common technique for measuring animal energetics in the field because the method permits the estimation of the rate of CO₂ production (rCO₂), which is an indicator of the metabolic rate in subjects (Lifson and McClintock 1966, Nagy 1980, Speakman 1997). The DLW method has been used to measure FMRs of many free-ranging animals (Nagy et al. 1999, Ellis and Gabrielsen 2002, Speakman and Król 2010). When water labeled with stable isotopes of oxygen and hydrogen (¹⁸O and ²H) is injected into a subject, the isotopes equilibrate in the body water pool, then are eliminated mainly as CO₂ and H₂O. Since ²H leaves as H₂O from subject, while ¹⁸O leaves as CO₂ and H₂O from subject, it is possible to estimate rCO₂, from the difference in elimination constants, which can then be used to calculate to metabolic rate (Figure 1.3A). The method, however, has been believed to be too imprecise to estimate the energy expenditure of an individual subject (Butler et al. 2004). Indeed, in the DLW method, random error generated through analytical variability can reduce the precision of estimated metabolic rate (Nagy 1983). Since both the initial and final sample add analytical variability of isotope ratio mass-spectrometry (IRMS), the variability

propagates and influence randomly calculated elimination rates and $r\text{CO}_2$ (Figure 1.3B-D). Thus, the DLW method has been mainly limited to provide a mean estimated metabolic rate of a group of individuals, which would have a mean error within about 2-3% (Butler et al. 2004, Speakman 1997). To make individual-based estimates and activity-specific metabolic rates feasible, it is necessary to reveal the causes of the individual discrepancies between an estimate in the DLW method and actual energy expenditures (Butler et al. 2004).

1.4. Aims and structure of the thesis

The main aim of this thesis is to understand the proximate mechanisms of adjustment of reproductive performance in relation to stochastic marine environments employed by a long-lived seabird, the streaked shearwater *Calonectris leucomelas*. The research incorporates measurements of chick growth, and parental energy expenditure and foraging and provisioning behaviors, to assess the birds' investment in the current reproductive attempt. To this end, I used activity tracking of individual birds with miniature data-loggers and measurement of their energy expenditure using the DLW method, which I validated using respirometry.

In Chapter 2, I examine the validity of the DLW method for the measurement of individual FMR in streaked shearwaters. In Chapter 3, I investigate the energetics of shearwaters' foraging behavior in relation to changes in the marine environment. I then explore how streaked shearwaters respond during their current reproductive attempt to a variety of breeding conditions, induced experimentally by increasing their cost of flight. Finally, in Chapter 4 I highlight the main results presented in this thesis and discuss their overall significance within a life history context.

1.5. Study species and area

The streaked shearwater (Figure 1.4) is a member of the order Procellariiformes, which comprises four families: albatrosses (Diomedidae), petrels and shearwaters (Procellariidae), storm petrels (Hydrobatidae), and diving petrels (Pelecanoididae; Warham 1990). It is a medium-sized seabird with a mean weight of ca. 500–600 g, with a large wing span of ca. 110 cm (Warham 1996). The islands on which this species breeds are distributed from 24-42°N and 121-142°E in East and Southeast Asia (Oka 2004). The longevity record of this species is 36 years (Yamashina Institute for Ornithology / Ministry of Environment 2012).

Streaked shearwaters return to their breeding colonies in mid-March, following a migration to tropical regions (Yamamoto et al. 2010). They nest in burrows and lay a single egg in mid- to late June (Yoshida 1981). The incubation period is 45-58 days (Yamamoto et al. 2012). Chicks hatch in early to mid-August, followed by a chick-rearing period of three months (Oka et al. 2002). Chicks attain their maximum body mass, approximately 130% of adult mass, in mid-October, and then lose mass, presumably coinciding with a reduction in the frequency of meals delivered by parents (Oka et al. 2002).

The species exhibits sexual dimorphism: males are larger than females (Arima and Sugawa 2004, Ochi et al. 2010). However, foraging areas during incubation do not differ between genders (Yamamoto et al. 2011). During the chick-rearing period, the parents' foraging trip duration varies widely, from one to more than 10 days (Ochi et al. 2010). They forage in offshore areas up to 800 km from their breeding colonies (Matsumoto et al. 2012, Ito et al. 2013). Streaked shearwaters feed on pelagic fish such as Japanese anchovy *Engraulis japonicus*, Pacific saury *Cololabis saira*, and jack-mackerel *Trachurus japonicus* (Kurasawa et al. 2012, Matsumoto et al. 2012), and

return to the colony only at night to provision their chick (Shiomi et al. 2012). Both parents share breeding duties (Ochi et al. 2010), and except for the early chick-rearing period (Lee and Yoo 2004), respond little to chick body condition (Inoue et al. 2009, Ogawa et al. 2015), as with other shearwater species (Riou et al. 2012). They are thus an excellent research model for studying flexibility in parental investment in relation to fluctuations in breeding conditions, because their life history traits enable us to eliminate complicating factors that originate from interactions among brood-mates, such as sibling competition, and conflicts between parents and chicks, such as adjustments according to the chick's needs (Wells 2003).

All experiments were conducted on Awashima Island (38°27'N, 139°13'E) in Niigata Prefecture, Japan (Figure 1.5). Awashima Island is located in the Sea of Japan, approximately 60 km north of Niigata City, within the warm Tsushima Current. The island is 6.1 km long and 4.4 km wide at its maximum, with an area of 9.86 km². The human population of the island is around 300, and predation by feral cats on streaked shearwaters has been reported there (Shiozaki et al. 2014).

The streaked shearwater population on the island was estimated to be 6,000-10,000 birds in 1990 (Oka 2004), and has tended to increase (60,000-84,000 birds in 2009, Maki Yamamoto, pers. comm.). The breeding colony is located in the western part of the island, at about 50-100 m in elevation, with 20-35° slopes. Burrow densities vary in the range 0.3-1.5 nests m⁻². The vegetation in the breeding colony is mainly *Fallopia japonica*.

This work was conducted with permits from the Ministry of the Environment, and all experiments were performed according to a protocol approved by the Institutional Animal Care and Use Committee of Nagoya University.

1.6. Figures

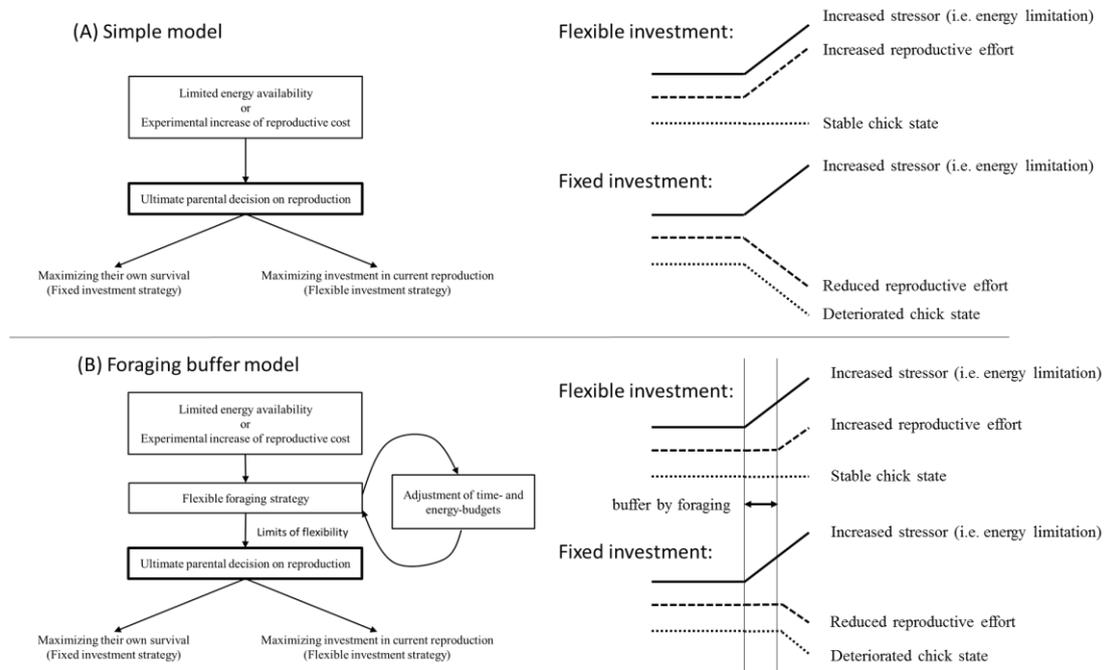


Figure 1.1.

Schematics illustrating study hypotheses. (A) The simple model states that stressors contribute directly to decisions about investment strategies. This hypothesis is used to predict the responses of individuals that work close to their intrinsic metabolic ceiling and have little flexibility in foraging strategy. (B) The foraging buffer model states that flexible foraging strategies are matched to fluctuating levels of energy availability or experimentally induced increases in energetic costs, and buffer negative consequences on both chicks and parents. Y-allocation trees illustrate the different resource allocation decisions depending on investment strategies (after Schultner et al. 2013)

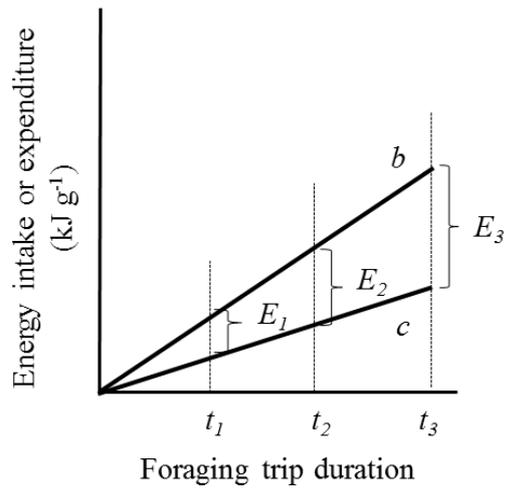
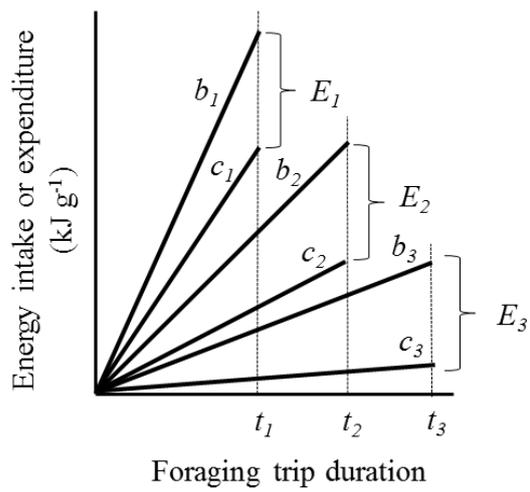
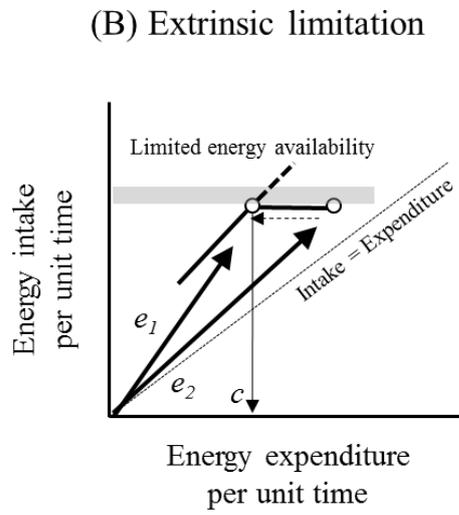
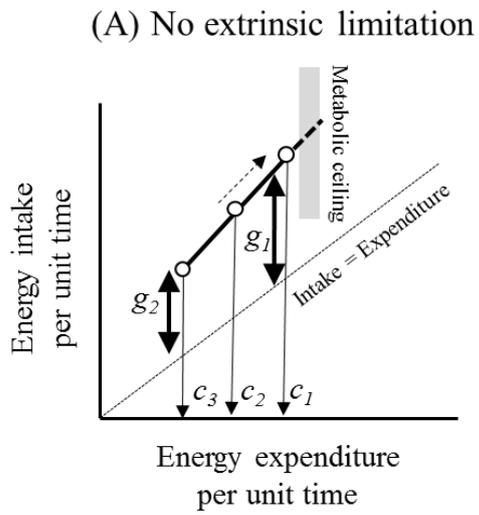


Figure 1.2.

The basic feeding models for central-place foragers in the absence of (A) and with (B) limited energy availability, based on the model of Ydenberg et al. (1994). The parameters b , c and t represent energy intake and expenditure rates, and foraging trip duration, respectively, while g , e and E represent net rate of gain, energy efficiency and net energy intake, respectively. (A) Animals are predicted to increase their energy expenditure rate up to their intrinsic metabolic ceiling if they can acquire more energy than they expend (upper panel). Under these conditions, adults can increase their net rate of gain ($g_1 > g_2$), although their energy efficiency may decrease. The increase in the net rate of gain contributes to an increase in the rate of energy delivery to offspring ($t_1 < t_2 < t_3$) while net energy intake is maintained ($E_1 = E_2 = E_3$; lower panel). (B) When energy availability is limited, reducing foraging effort may be more beneficial for optimizing the net rate of gain, and may lead to an increase in energy efficiency ($e_1 > e_2$; upper panel). Because of a relatively fixed energy intake rate, and consequently net rate of gain, individuals may be forced to perform longer foraging trips ($t_1 < t_2 < t_3$) to ensure an increase in net energy intake ($E_1 < E_2 < E_3$; lower panel).

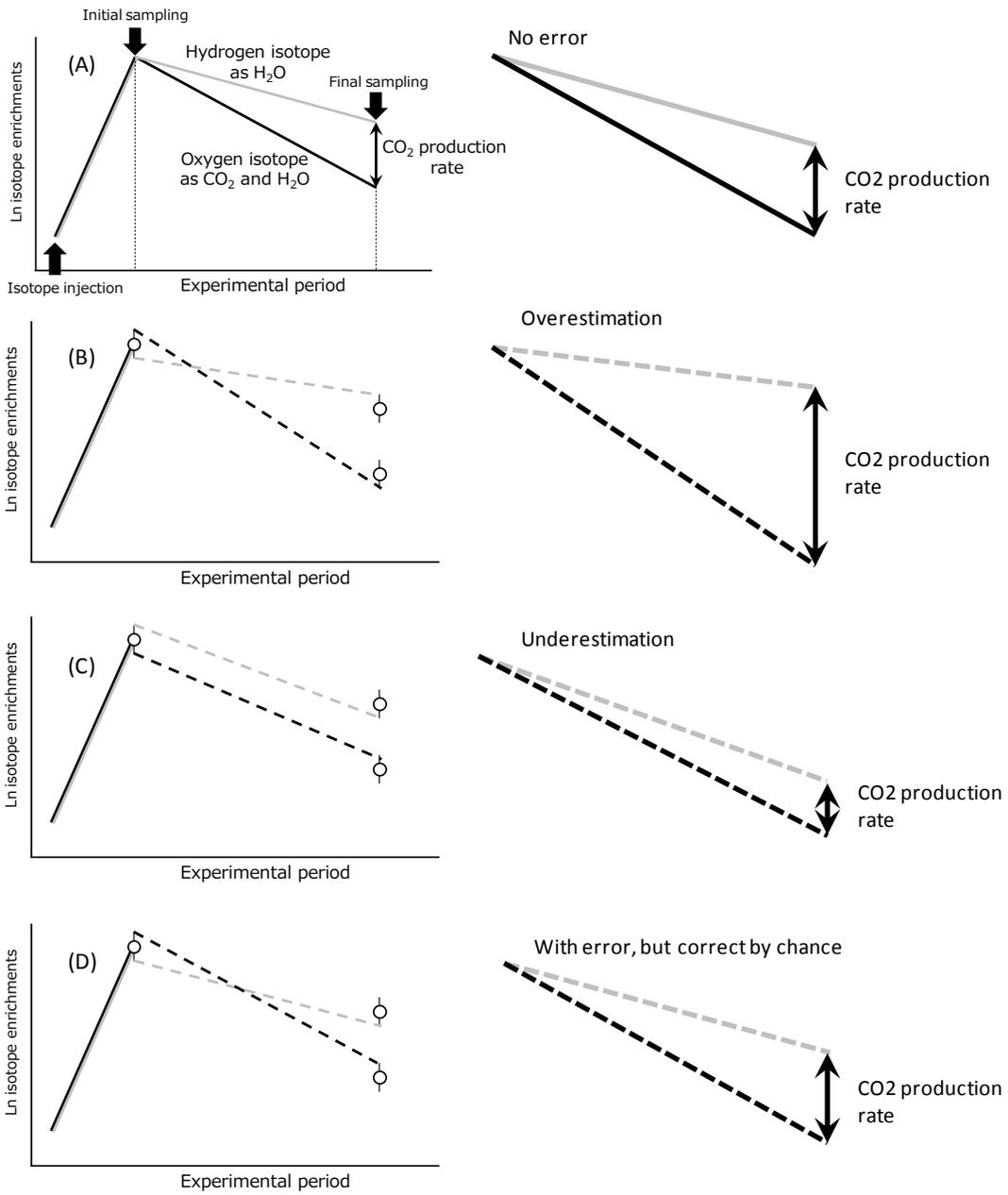


Figure 1.3.

Schematic diagram of the causes of random error through isotopic analytical variability on the doubly labeled water method. (A) Isotopes flood the body water leading to a sharp exponential increase in enrichment until equilibrium is reached. Following the equilibrium, the isotopes are eliminated down exponential routes back to the background levels. Because oxygen isotope (black line) is eliminated in both H₂O and CO₂, its enrichment declines faster than that of hydrogen isotope (grey line), which is eliminated only in H₂O. The difference in the isotope elimination rates provides a quantitative estimate of the rates of CO₂ production. (B-D) Each isotope enrichment (open circle) of initial and final isotopes receives analytical variability of isotope ratio mass spectrometry (vertical solid line stuck on the open circle). The isotopic analytical variability causes a discrepancy between the actual and estimated CO₂ production rates, which are provided from difference in the uncertain isotope elimination rates (black and grey dashed lines). Estimated CO₂ production rates were largely (B) overestimated or (C) underestimated by the inverse analytical errors of initial and final sample. (D) However, because CO₂ production rates were computed by the “rate” of isotope eliminations, there is little error on estimated CO₂ production when the directions of the analytical errors correspond. Therefore, the propagations of analytical errors influence randomly estimated CO₂ production rates.



Figure 1.4.

Streaked shearwater *Calonectris leucomelas* at its burrow entrance on Awashima Island, Niigata, Japan.



Figure 1.5.

Location of Awashima Island, in the Sea of Japan.

Chapter 2:

Applicability of the doubly labeled water method for individual-based measurements of metabolic rates in animals

2.1. Introduction

The balance between energy acquisition and energy expenditure strongly impacts survival and reproductive success of animals (Kitaysky et al. 2000, Ricklefs and Wikelski 2002, Golet et al. 2004). Individual variations in field metabolic rate (FMR) are often large (e.g. Fyhn et al. 2001, Welcker et al. 2010) and may influence reproductive performance (e.g. Wendeln and Becker 1999), so an individual's ability to adjust energy expenditure might, therefore, be a good predictor of fitness (Drent and Daan 1980, Peterson et al. 1990). Even so, limited studies have investigated the proximate factors of individual variation of energy expenditures in wild animals (Bryant and Tatner 1991, Tinbergen and Dietz 1994, Scantlebury et al. 2014), mainly because of the limitations of the methodologies available for measuring energy expenditure in free-living animals (Butler et al. 2004).

Although the doubly labeled water (DLW) method has been believed to be too imprecise to estimate the energy expenditure of an individual subject (Butler et al. 2004), there are some attempts to examine the relative contribution of intra- and inter-individual differences on FMR measured via the DLW method (Speakman et al. 1994, Berteaux et al. 1996 Williams et al. 2009, Elliott et al. 2014). Some field studies using the DLW method, particularly studies of pelagic seabirds, show correlations between individual FMR and behaviour or with environmental variables. For example, FMR in thick-billed murre *Uria lomvia* is strongly positively correlated with locomotion intensity measured by a miniature accelerometer (Elliott et al. 2013b). In wandering albatrosses *Diomedea exulans*, FMR increases with increase of landing number (Shaffer et al. 2001). Unsuitable wind conditions for flight also increase FMR in some seabirds (Furness and Bryant 1996, Mullers et al. 2009). A computer simulation study of the precision of the DLW method was conducted using an artificial FMR data

set of snakes with a randomly generated factor between -20% and +20% (Appendix in Peterson et al. 1998). The result suggests that despite a possible discrepancy of individual FMR measurements of up to 20%, individual FMR correlates with other ecological variables (Peterson et al. 1998). This evidence suggests that FMR measured by the DLW method may have sufficient precision to detect correlations between energy expenditure and individual activity or with environmental variables (Shaffer 2011).

Since DLW measurements in the field are conducted over the course of longer experimental periods, one might expect that subjects in field studies eliminate much larger quantities of isotope than subjects in validation studies. In fact, in DLW experiments, a high level of isotope eliminations is recommended at least until isotope levels of a subject become close to natural isotope abundance because increased isotope eliminations are expected to make the isotopic analytical variability (i.e. random error) smaller than the amount eliminated and should therefore generate more reliable isotope elimination rates (Nagy 1983). The validation study in California sea lions *Zalophus californianus*, which resulted in isotope depletions of 9.0% in ^2H and 13.8% in ^{18}O , produced a mean coefficient of variation (%CV) of 35% in DLW estimates (Boyd et al. 1995), whereas a study in grey seals *Halichoerus grypus* accompanied with isotope depletions of 38% in ^2H and 46% in ^{18}O produced a mean %CV of 7% (Sparling et al. 2008). Metabolic rates in a poultry chick measured over four days (mean absolute errors [i.e. precision]: 3.9-6.9%) was more precise than that measured over just one day (10.5-17.0%) (Gessaman et al. 2004). In addition, metabolic rates in little penguins *Eudyptula minor* estimated from the DLW method were 10.9% higher than those estimated from a material balance after 2 days, but only 1.7% higher after 6 days (Gales 1989). Although these observations imply that improved precision and/or accuracy of the DLW method by high isotope eliminations may allow reliable measurements of

individual differences by the DLW method in the field, few validation studies have investigated the actual precision and accuracy on the DLW method considering situations in the field.

To investigate the precision and accuracy of the DLW method under an environment where a subject experiences different levels of isotope elimination, I measured metabolic rate in streaked shearwaters using the DLW method, simultaneously with the respirometry. Experimental periods and conditions, expected to affect isotope elimination, were changed among experimental groups. I examined how the amount of eliminated isotope affects the precision and accuracy of metabolic rate measured by the DLW method.

2.2. Materials and Methods

This experiment was conducted between August and October in 2010, 2012 and 2013. I caught 24 adult shearwaters (10 birds in 2010, five birds in 2012 and nine birds in 2013) at night in their burrows to obtain their metabolic rates measured by both the respirometry and DLW method. The captured birds were divided into three groups, which were subjected to experiments of different conditions that were expected to produce different amount of isotope elimination. Group A (10 birds) was used for a measurement at rest on the ground for 24-hour (10 birds), whereas Group B (5 birds) for a measurement at rest on the ground for 48-hour. In seabirds, metabolic rates while resting on the water is expected to be two or three times larger compared to when they are just resting on the ground (Bevan et al. 1995a, Richman and Lovvorn 2011). Group C (9 birds) was, thus, used for a measurement at rest on the water for 24-hour. Each bird was held in dark boxes, transported to the laboratory within 10 min and kept for at least two hours to minimize the effects of capture stress on the metabolic rate. After the

experiment, the birds were immediately released back into their burrows and given a supplementary feeding of approximately 20 g of Japanese jack mackerel *Trachurus japonicus*. I also captured 22 other adult birds not used in the respirometry and DLW experiment (four birds in 2010 and nine birds in 2012 and 2013) and took 1 ml of blood to determine the natural background isotope abundances in each year.

Respirometric method

Oxygen consumption rate (\dot{V}_{O_2}) during the entire 24-hour or 48-hour period was measured using an open-flow respirometry system consisting of an acrylic metabolic chamber and an oxygen analyzer (Xentra 4100; Servomex, Crowborough, UK; Shirai et al. 2012). For the measurement of metabolic rate on the ground, a 20-L metabolic chamber (20 cm long \times 25 cm high \times 40 cm wide) was submerged in a thermostatic water bath and maintained at $20.8 \pm 0.8^\circ\text{C}$ (mean \pm SD). Measurements of metabolic rate of birds on the water were obtained by filling a 72-L metabolic chamber (30 cm long \times 60 cm high \times 40 cm wide) with freshwater to a depth of 30 cm while the temperature of the water was maintained at $21.4 \pm 1.7^\circ\text{C}$. Absorption of oxygen by water in the chamber was assumed to be negligible (less than 0.0015% per minute according to Allers and Culik [1997]). The chamber temperature (T_c) and atmospheric pressure (P_a) were recorded using loggers (T_c : $\pm 0.7^\circ\text{C}$, Thermochron Type-SL; KN Laboratories, Ibaraki City, Osaka, Japan; P_a : ± 1.5 hPa, TR-73U Thermo Recorder; T&D Corp., Matsumoto City, Nagano, Japan) every minute. The flow rate through the chamber was maintained at 2.0 L min^{-1} (on the ground) and 5.0 L min^{-1} (on the water) using a mass flow controller calibrated by the manufacturer using hydrogen gas with a controlled flow rate ($\pm 2\%$, Type HM1171A; Tokyo Keiso, Minato City, Tokyo, Japan). The effluent air was dried using a water separator (AMG150C, SMC Co., Tokyo, Japan)

and silica gel, and a fraction of the dry effluent air was directed into the oxygen analyzer. The oxygen analyzer was calibrated using dry ambient air (set to 20.946% oxygen) and pure stock nitrogen (set to 0.000% oxygen). The oxygen concentration in the effluent air was automatically recorded every minute. \dot{V}_{O_2} was calculated using formula 3A presented by Withers (1977). I assumed that the respiratory exchange ratio (RER) was 0.8, which minimizes error in the estimated rate of energy expenditure when RER is unknown (Koteja 1996), and that the oxygen concentration of influent air was 20.946%. Assuming that the RER is 0.8, the error of the estimated rate of oxygen consumption is between -2.6% and +4.4% when the actual RER is between 0.7 and 1.0 (Koteja et al. 1996). Initial (BM_i) and final body masses (BM_f) were measured using a spring scale (Pesola, Baar, Switzerland) with a scale division of 10 g and estimated to the nearest gram before and after the bird was placed in the respirometric chamber, respectively. The body mass was assumed to decrease linearly from BM_i to BM_f . A conversion coefficient of 20.1 kJ L^{-1} was used in calculating the energy expenditure from \dot{V}_{O_2} (RER = 0.8; [Gessaman and Nagy 1988]). Each bird's energy expenditure was recorded every minute and these values were used to calculate the total energy expenditure for the whole duration of the experiment to allow comparison with energy expenditures measured using the DLW method.

For comparison with previous published data, I calculated mass-specific resting metabolic rates (RMR) on the ground and on the water. Although previous publications used the term of BMR, RMR or SMR to describe the baseline of energy metabolism, this study treat all these measures of resting metabolism as equivalent, and use RMR to represent resting metabolism. Since metabolic rate, even during resting, may be affected by slight changes in body temperature, hormone levels and a host of other underlying physiological processes, shorter calculation intervals may lead to high stochastic

variance (Hayes et al. 1992). On the other hand, longer calculation intervals may include periods of activity (Hayes et al. 1992). Thus, I calculated the minimal metabolic rate of the shearwater with a 30 min interval. All results are given at standard temperature and pressure for dry gas (STPD).

Procedure for doubly labeled water method

Each shearwater was injected intraperitoneally with 2.5-3.0 g of DLW containing 10.2-12.2 atom-percent ^{18}O (Taiyo Nippon Sanso, Shinagawa City, Tokyo, Japan), 5.5-5.8 atom-percent ^2H (Isotech, Miamisburg, OH, USA) and 0.9% NaCl. To quantify the injected dose, the syringe was weighed before and after injection on an electrical balance (Mettler-Toledo, Columbus, OH, USA) to the nearest 0.1 mg. After the injection, the bird was placed into a plastic box for 160-180 min to allow the injected dose to equilibrate. Then, 1 ml of blood was taken from the brachial or tarsal vein of the bird (initial sample), and the bird was placed in a respirometric chamber. To reduce the error caused by circadian metabolic rhythm, measurement period was adopted as a multiple of 24 hours (Speakman and Racey 1988). Twenty-four or forty-eight hours after taking initial samples, the bird was removed from the chamber, and 1 ml of blood was taken from the brachial or tarsal vein (final sample).

Each blood sample was put into a heparinized tube and centrifuged immediately (5 min, 6200 rpm). The serum was then transferred to a plastic screw-cap vial with O-rings (AGC Techno Glass, Funabashi City, Chiba, Japan) and frozen at -25°C until isotope ratio analysis.

Isotope ratio analysis

The hydrogen (^2H) and oxygen (^{18}O) isotopic compositions of the serum and

DLW dose samples were analyzed according to the procedure of Shirai et al. (2012) using isotope ratio mass spectrometry (IRMS; Hydra 20-20, Sercon, Crewe, UK; [Yamada et al. 2009]). The dose and serum samples were diluted with distilled water using an electrical balance (Mettler-Toledo, Columbus, OH, USA) to the nearest 0.01 mg (Shirai 2012). The concentration of distilled water was measured using the IRMS, as with the diluted serum and dose samples.

The distilled water, diluted serum and dose samples were put into cylindrical tubes and analyzed using the water equilibration method (Horita et al. 1989). Water standards (Iso-Analytical, Crewe, UK) were used to establish calibration curves for normalizing the values. Each sample was analyzed in duplicate. All isotope concentrations were measured in δ per mille relative to the working standards and converted to ppm. All subsequent calculations in the DLW method were performed on the mean values of each sample analyzed in duplicate.

Calculations in the DLW method

The plateau method was used to determine the isotope dilution spaces for hydrogen (N_d , mol) and oxygen isotopes (N_o , mol), and to estimate total body water (TBW) pool (Speakman 1997, Jacobs et al. 2012). For the calculations of $r\text{CO}_2$, the dilution space ratio ($R_{dilspace}$) was also obtained as N_d/N_o (Speakman 1997). The elimination rates for hydrogen and oxygen isotopes (k_d and k_o , respectively, day^{-1}) were determined using the two-sample technique (Lifson and McClintock 1966, Speakman 1997).

Ideally, background isotope levels should be determined for each animal before injection with labeled water (Speakman and Racey 1987). However, this increases both the handling time and disturbance to the animal. Thus, I determined the natural

background isotope abundances in 22 uninjected adult shearwaters. I used the mean background levels of each year to calculate the CO₂ production rate (rCO₂, ml day⁻¹) (see Appendix Table S2.2).

RCO₂ was calculated for each trial using several different published models with different assumptions about evaporative water loss and different combinations of body water pool estimates. The calculation models are largely categorized into two types based on different assumed body temperatures (25°C or 37°C; Speakman [1997]). I used the following five equations including isotope fractionation factors measured at 37°C, because an assumed body temperature of 37°C is more realistic for streaked shearwaters (40.5°C; Warham [1996]). Since the subjects did not receive any food during the experiment, for the rCO₂ calculation, I averaged the values of initial and final body water pools as the body water pool of each subject considering their body mass loss. I inferred the value of final isotope dilution space from the final body mass, assuming the same percentage of body water pool as measured for the initial body water pool.

One-pool model by Speakman (Speakman 1997) (SP97 one-pool):

$$rCO_2 = \left(\frac{N}{2.078} \right) \cdot (k_o - k_d) - 0.0062k_d N,$$

$$\text{where } N = N_o \cdot \left(\frac{BM_i + BM_f}{2BM_i} \right).$$

Two-pool model by Schelloer et al. (Schoeller et al. 1986) (SCH86), as modified by Schoeller (1988):

$$rCO_2 = \left(\frac{N}{2.078} \right) \times (1.01k_o - 1.04k_d) - 0.246N1.05(1.01k_o - 1.04k_d),$$

$$\text{where } N = \frac{(N_o / 1.01) + (N_d / 1.04)}{2} \cdot \left(\frac{BM_i + BM_f}{2BM_i} \right).$$

Two-pool model by Speakman et al. (Speakman et al. 1993) (SNG93):

$$rCO_2 = \left(\frac{N}{2.078} \right) \times (1.01k_o - 1.0532k_d) - 0.246N(1.01k_o - 1.0532k_d),$$

$$\text{where } N = \frac{(N_o / 1.01) + (N_d / 1.0532)}{2} \cdot \left(\frac{BM_i + BM_f}{2BM_i} \right).$$

Two-pool model by Speakman (1993) (SP93):

$$rCO_2 = \left(\frac{N}{2.078} \right) \times (k_o - R_{dilspace}k_d) - 0.246N1.05(k_o - R_{dilspace}k_d),$$

$$\text{where } N = \frac{(N_o + N_d / R_{dilspace})}{2} \cdot \left(\frac{BM_i + BM_f}{2BM_i} \right).$$

Two-pool model by Speakman (Speakman 1997) (SP97 two-pool):

$$rCO_2 = \left(\frac{N}{2.078} \right) \times (k_o - R_{dilspace}k_d) - 0.0062NR_{dilspace}k_d,$$

$$\text{where } N = \frac{(N_o + N_d / R_{dilspace})}{2} \cdot \left(\frac{BM_i + BM_f}{2BM_i} \right).$$

The water efflux (rH_2O , ml day⁻¹) is equal to the sum of the water loss from respiration, skin and excreta, and was computed using the elimination rate of hydrogen isotope from the equation of Bevan et al. (1995b) (based on Nagy and Costa [1980]) as follows:

$$rH_2O = \frac{(N_f - N_i) \cdot \ln[(H_i \cdot N_i) / (H_f \cdot N_f)]}{\ln(N_f / N_i) \cdot t}$$

$$\text{where } N_i = 18.002 \cdot \frac{(N_o + N_d / R_{dilspace})}{2}, \text{ and } N_f = N_i \cdot \left(\frac{BM_f}{BM_i} \right).$$

H_i (ppm) and H_f (ppm) are the initial and final concentrations of hydrogen isotope, respectively, and t (days) is the time between initial and final blood sampling being taken. To convert units in ml day^{-1} into energy equivalents, I assumed that $1 \text{ ml of CO}_2 = 25.11 \text{ J}$ (RER = 0.8; [Gessaman and Nagy 1988]).

Data analysis

To estimate metabolic rate via the DLW method, two or three replicate analyses are generally used to calculate the mean isotope values (Speakman 1997). These replicate analyses give an indication of the isotopic analytical variability (i.e. the magnitude of random error) in estimates of metabolic rate within individual (Speakman 1995). In this study, because the initial and final concentrations of oxygen and hydrogen isotopes were analyzed in duplicate, respectively, the number of potential combinations in calculated metabolic rate is $2^4=16$ estimates (two initial and two final samples in both oxygen and hydrogen isotopes) in each individual. The confidence intervals (95% CIs) and standard deviation of estimated metabolic rates were obtained using the 16 estimates. The coefficient of variation (%CV) was calculated by dividing the standard deviation by the metabolic rate calculated using the mean isotope values from two replicate analyses.

To compare the DLW method and respirometry, I used Passing-Bablok regression analysis to provide unbiased linear regression slopes and intercepts (Passing and Bablok 1983). Unlike ordinary least-squares regression, the Passing-Bablok regression analysis allows for imprecision in both the reference method (e.g. the respirometry) and the comparison method (e.g. the DLW method). There are two potential sources of systematic disagreement between methods of measurement: fixed and proportional error (Ludbrook 1997). For fixed error, one method gives values that

are higher (or lower) than those from the other by a constant amount. For proportional error, one method gives values that are higher (or lower) than those from the other by an amount that is proportional to the level of the measured variable. Fixed error is indicated if the 95% confidence interval (CI) for the intercept of the Passing-Bablok regression does not include zero. Proportional error is indicated if the 95% CI for the slope of the Passing-Bablok regression differs from unity.

All data were analyzed using R version 3.0.1. (R Core Team 2013). I used t-tests (two tailed), ANOVA with Tukey's HSD multiple comparison test and Passing-Bablok regression analysis. Passing-Bablok regression was run using the "mcreg" function in mcr package (Manuilova et al. 2015). Statistical analyses of %CV were performed after the data were arcsine-transform. I report this results without Bonferroni or similar adjustments on *P* values (see Rothman 1990, Perneger 1998). *P* values of less than 0.05 were considered statistically significant. All mean values are presented \pm SD.

2.3. Results

Energy expenditures measured by respirometry (TEE_{resp}) ranged from 238.7 to 1137.0 kJ (see Appendix Table S2.1). TEE_{resp} in Group B and C was on average 1.9 and 3.3 times higher than that in Group A (Table 2.1). In Group B, there was statistically no difference in the TEE_{resp} between the first and the second 24-hours ($t_4 = 1.40$, $P = 0.1$). Mass-specific resting metabolic rates measured by respirometry (RMR_{resp}) was significantly different among the groups (Table 2.1). I found no statistical difference in RMR_{resp} measured on the ground between 2010 vs. 2013 ($t_{13} = 0.18$, $P = 0.9$), or in RMR_{resp} measured on the water in 2012 vs. 2013 ($t_7 = 0.89$, $P = 0.4$). RMR_{resp} measured on the water ($0.0519 \pm 0.011 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$; $n = 9$) was to 3.4 times higher than RMR_{resp} on the ground (combined Group A and B $0.0154 \pm 0.0021 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$; $n = 15$).

Initial isotope concentrations in Group A, B and C were 626.3 ppm (± 41.5 , $n = 10$), 548.9 ppm (± 43.8 , $n = 5$) and 554.5 ppm (± 46.6 , $n = 9$) in ^2H , respectively. In ^{18}O , initial isotope concentrations in Group A, B and C were 2886.5 ppm (± 57.3 , $n = 10$), 2870.1 ppm (± 102.5 , $n = 5$) and 2861.0 ppm (± 111.2 , $n = 9$), respectively. The depletion of ^2H of body water from the initial concentrations was on average 6.1% (± 5.1 , $n = 10$) in Group A, 7.8% (± 1.9 , $n = 5$) in Group B, and 33.4% (± 15.0 , $n = 9$) in Group C, respectively (see Appendix Table S2.2). Similarly, the depletion of ^{18}O of body water from the initial concentrations was on average 11.5% (± 4.3 , $n = 10$) in Group A, 17.8% (± 2.0 , $n = 5$) in Group B, and 46.6% (± 14.8 , $n = 9$) in Group C, respectively (see Appendix Table S2.2). The elimination rate of hydrogen (k_d) and oxygen isotope (k_o) in Group C was significantly higher than all other conditions, but the k_d/k_o ratios did not differ among the groups (Table 2.1). The water efflux rate in Group C was also significantly higher than in all other conditions (Table 2.1).

TEE_{resp} , along with corresponding total energy expenditures measured by the DLW method (TEE_{dlw}) and the ratio between the two estimates are detailed in Table 2.2 (see Appendix Table S2.3 for individual values). Regardless of the equations, mean value of TEE_{dlw} in Group A matched with TEE_{resp} (Table 2.2). In Group B and C, the equation by Speakman et al. (1993; two-pool model) provided the most accurate TEE_{dlw} , whereas the equation of Speakman (1997; one-pool model) provided the least accurate results (Table 2.2). Mean TEE_{resp} corresponded to 104%, 81% and 76% of mean TEE_{dlw} calculated by the equation by Speakman et al. (1993) in Group A, B and C, respectively (Table 2.2).

For all calculations of precision and accuracy for the DLW method, I used the results from the two-pool model of Speakman et al. (1993) (see Appendix Table S2.4). The %CVs (relative impacts of isotopic analytical variability on energy expenditure) of

TEE_{dlw} in Group B were significantly lower than with those in Group A ($t_{13} = 2.47$, $P = 0.037$; Figure 2.1). The %CVs in Group C also tended to be lower than those in Group A, but the difference was not significant ($t_{17} = 2.12$, $P = 0.0503$; Figure 2.1).

To test the linearity between the DLW method and respirometry, six combinations of groups (A, C, A-B, A-C, B-C and A-B-C) were tested for agreement between the DLW method and respirometry by Passing-Bablok regression analysis, except for Group B because of its small sample size. Among all tests, the combination of Group B and C is the best model, which is the closest to identical to the estimates obtained from respirometry (Figure 2.2, Table 2.3). The coefficient of determination (R^2) of the best model is 0.82. Although the best model showed the intercept value with insignificant fixed error, the slope value was significantly overestimated and differed from unity (Table 2.3).

2.4. Discussion

I used two indices to measure the reliability of the DLW method: precision (i.e. the closeness of repeated measurements within an individual) and accuracy (i.e. the closeness of an estimated value to respirometry). The mean resting metabolic rates on the ground measured by respirometry (RMR_{resp}) ($0.0154 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) was equal to the predicted RMR ($0.0155 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) that was calculated (using body mass = 500 g) from equation 11.6 from Ellis and Gabrielsen (2002). Similarly to seabirds such as cormorant, shag and penguin that show RMRs on the water to be over three times higher than RMR on the ground (reviewed in Richman and Lovvorn [2011]), I found that sitting in water increased RMR_{resp} in streaked shearwaters by a factor of 3.4 and also increased the elimination rates of hydrogen and oxygen isotopes (k_d , k_o) and water efflux rate. With regard to the accuracy of the DLW method, mean TEE_{dlw} matched mean total energy

expenditures measured by respirometry (TEE_{resp}) in Group A, whereas TEE_{dlw} was overestimated in Group B and C compared with TEE_{resp} . The TEE_{dlw} in Group B and C, however, showed higher precision (i.e. less random error) for the DLW method than the TEE_{dlw} estimates derived in Group A. Although the best regression model (No. 1 in Table 2.3) detected systematic (proportional) error between TEE_{dlw} and TEE_{resp} , the analysis also showed a high correlation between the methods. This study clearly demonstrates that differences in experimental design influence both the precision and accuracy of the DLW method through random and systematic errors.

Differences of precision depending on experimental conditions

Compared with Group A, TEE_{dlw} in Group B and C had lower isotopic analytical variability (i.e. random error) (Figure 2.1), but also had lower accuracy (see below). This indicates that relative high isotope elimination alleviates the effects of analytical variability of IRMS on TEE_{dlw} and improves the precision of the DLW method, as found by Sparling et al. (2008). Nagy (1980) and Gales (1989) recommended that the final oxygen isotope concentration above background should be lower than approximately 50% of the initial concentration above background to reduce the effects of errors in isotopic analysis, as supported by this result from Group C. Almost all previous DLW validation studies have not counted or described the extent of eliminated isotopes, so the degree to which their results are influenced by the random error in isotopic analysis is not known.

Presumably because the impact of analytical variability on TEE_{dlw} was reduced in Group B (longer experiment period) and C (measured on water), the best regression model (Group B and C, No. 1 in Table 2.3) showed a high correlation between TEE_{dlw} and TEE_{resp} . This result is consistent with a previous simulation study of DLW method

precision, which concluded that inter-individual comparisons in relation to ecological variables by the method are robust (Peterson et al. 1998). Several validation studies have advised caution that individual estimates from the DLW method can differ by more than 40% from those derived from the respirometry method (Bevan et al. 1995b, Boyd et al. 1995, Jones et al. 2009). The experimental design and species used for these validations (turtle and water bird), however, have some disadvantages for applying the DLW method: relative short experimental period (Boyd et al. 1995) and high water efflux relative to CO₂ production (i.e. k_d/k_o ratio of 0.8 and above) and/or low metabolic rate (Bevan et al. 1995b, Jones et al. 2009). High water efflux relative to CO₂ production creates a situation where the difference in isotope turnover of hydrogen and oxygen is small (Jones et al. 2009). Thus, errors in isotopic analysis can easily influence calculated metabolic rates (see Figure 4 of Nagy [1980]). In this study, streaked shearwaters have different physiologies in that they are a homoeothermic with low k_d/k_o ratios (mean ratios: 0.454 in Group A, 0.410 in Group B and 0.619 in Group C). Thus, although a correction for systematic error is necessary for a valid estimation (see below), these results suggest that a high extent of isotope elimination provides DLW estimates with high precision, which may reflect relative individual estimates.

Differences of accuracy depending on experimental conditions

In agreement with many other validation studies of the DLW method (reviewed in Speakman [1997, 1998]), the mean TEE_{dlw} across the group of birds in Group A was close to the mean TEE_{resp} (Table 2.2), whereas TEE_{dlw} in Group B and C were highly overestimated by proportional error (Table 2.2, 2.3). The differences in accuracy depending on experimental conditions may be produced by the relative difference between random (e.g. impact of isotopic analytical variability on TEE_{dlw}) and

systematic error (e.g. disagree of mismatch between the assumptions of the DLW method and physiological conditions in streaked shearwater). Since random error within a group generally cancels itself out, it has little influence on the average of the group (Taylor 1997). Because the TEE_{dlw} in Group A includes relatively large isotopic analytical effect (Figure 2.1), the match between mean TEE_{dlw} and TEE_{resp} in Group A is consistent with the characteristics of random error. On the other hand, the TEE_{dlw} in Group B and C eliminated the random error by higher extent of isotope eliminations (see above), so the estimates may show systematic error. When the DLW method is used in the field, the situation (e.g. the extent of eliminated isotopes) more closely resembles conditions in Group B and C compared to Group A. Thus, the correction using the best regression model ($TEE_{dlw} = 1.37 TEE_{resp} - 14.12$; Table 2.3) may help to provide actual TEE of streaked shearwater in the field. The correction may be effective before three half-lives of oxygen isotope (i.e. one eighth of initial concentration; Nagy, 1983), because the elimination rate of oxygen isotope may change if the concentrations of the oxygen isotope at final sampling are too close to the concentrations at background.

What is the cause of the systematic error in streaked shearwater? The DLW method relies on distinguishing the elimination curves of oxygen and hydrogen isotopes (Figure 1.2). Thus, the overestimated TEE_{dlw} depends on the rates of isotope eliminations and suggests that the k_d was underestimated, the k_o was overestimated, or both processes occurred simultaneously. The best regression model showed proportional error, which suggests that the estimated isotope elimination rates constantly stray outside of the range of actual rates. With regard to k_d , the mean water efflux rates in individuals of Group A and B, which was measured by the k_d , was 32% above the level ($21.2 \text{ ml} \cdot \text{day}^{-1}$) predicted for birds based on the allometric equation with phylogenetic analysis (Williams 1996). Thus, for birds in both Groups A and B k_d is unlikely to be

underestimated. In Group C, water efflux rate increased 4.0 times compared with those in Group A and B, and the increment exceeded the level of the increment in metabolic rate (3.4 times). Therefore, although there is little information about water efflux rate in birds while floating on the water, this result suggested that for birds in Group C, I did not underestimate k_d . So, the overestimated TEE_{dlw} in both Group B and C may be caused by the overestimation of k_o . As the cause of the overestimation in k_o , previous studies pointed out the possibilities of additional irreversible loss of oxygen isotope to urea through the ornithine-arginine cycle (Sparling et al. 2008) or to ketone bodies (Guidotti et al. 2013). Although both the previous and present studies have not isolated the specific cause of the k_o overestimation, the cause of the systematic error may be partially due to additional substances by fasting condition in this experiments, which increase the production of ketone bodies such as β -hydroxybutyrate (Totzke et al. 1999).

As the other explanations for the systematic error of the DLW method, TBW might have caused the overestimated TEE_{dlw} . Since TBW estimated by isotope dilution method was used to calculate the TEE_{dlw} (see Materials and Methods), the error of TBW estimation would reduce the accuracy of the DLW method. However, previous studies suggest that TBW estimated by the isotope dilution method matched actual TBW in seabirds (accuracy: $-4.8 - +7.0\%$; Jacobs et al. 2012). Thus, although I have no actual TBW values for streaked shearwaters, the impact of TBW on the overestimated TEE_{dlw} should be limited.

These results suggest that the DLW method accurately estimates the mean metabolic rate of animals only in some circumstances (Butler et al. 2004, Speakman 1998). The DLW method, thus, should be used with caution especially when characterizing inter-species difference of FMR. Most of previous validation studies in birds, reptiles and mammals have been conducted under only one experimental

condition (i.e. fixed measurement period and metabolic rate of subjects) within a study (reviewed in Speakman [1997]). Further validation study is required to evaluate accuracy of the DLW method and to understand factors affecting the accuracy for a larger range of species.

2.5. Conclusion

The results indicate that the precision of the DLW method improves substantially in experiments designed to be more closely imitated after field conditions, i.e. longer sampling intervals or higher metabolic rate. This effect is primarily mediated by reduced isotopic analytical variability in the energy expenditure estimates produced by the DLW method. In these conditions, I found a high correlation between the total energy expenditure estimates derived by the DLW method and respirometry. The results support Shaffer's (2011) suggestions that individual DLW estimates partially contribute to a relative index of individual effort in free-ranging animals. However, with an overestimation of TEE_{dlw} of greater than 30% in situations with high isotope elimination implies that the method does not always provide accurate differences of energy expenditure between species. Since few validation studies have discussed the actual precision and accuracy of the DLW method for field use, this study emphasizes the need for further validation studies for the refinements and revisions of the usage of the DLW method in the field. Nevertheless, the recent dramatic increase in studies of alternative behavioral and resource allocation strategies has been fettered by the lack of a suitable method for quantifying individual differences in energy expenditure in free-living animals and this study indicate that the DLW method can perform adequately for such aims.

2.6. Figures and Tables

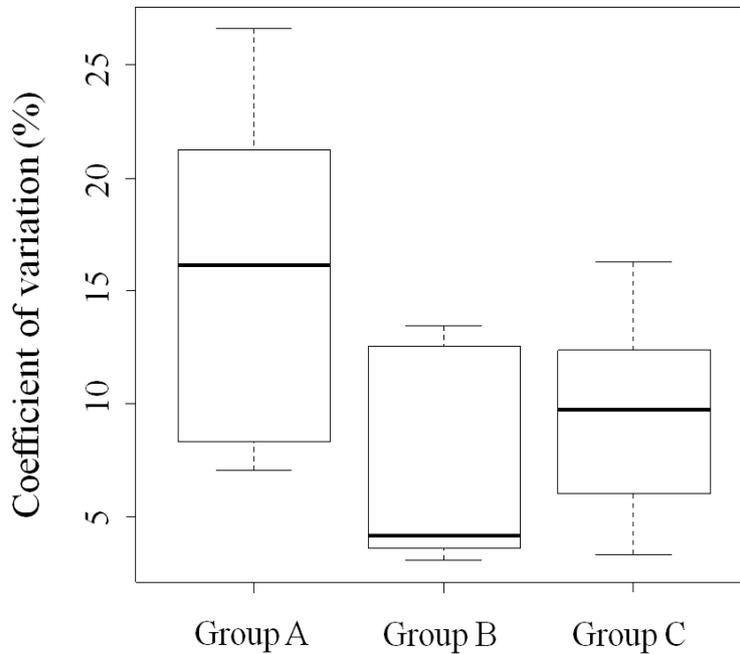


Figure 2.1.

Effect of isotopic analytical variability on total energy expenditures measured by the doubly labeled water method in streaked shearwater by three different experimental conditions: at rest on the ground for 24-hour (Group A; $n = 10$) or for 48-hour (Group B; $n = 5$), and at rest on the water for 24-hour (Group C; $n = 9$). Duplicate isotopic analyses of serum samples provided 16 calculated metabolic rates in each individual. The coefficient of variance of the 16 metabolic rates in each individual gives an indication of the isotopic analytical variability on metabolic rates measured by the doubly labeled water method. The coefficient of variation calculated in Group B was significantly lower than that in Group A ($P = 0.037$). Similarly, the coefficient of variation in Group C tend to be lower than that in Group A ($P = 0.0503$).

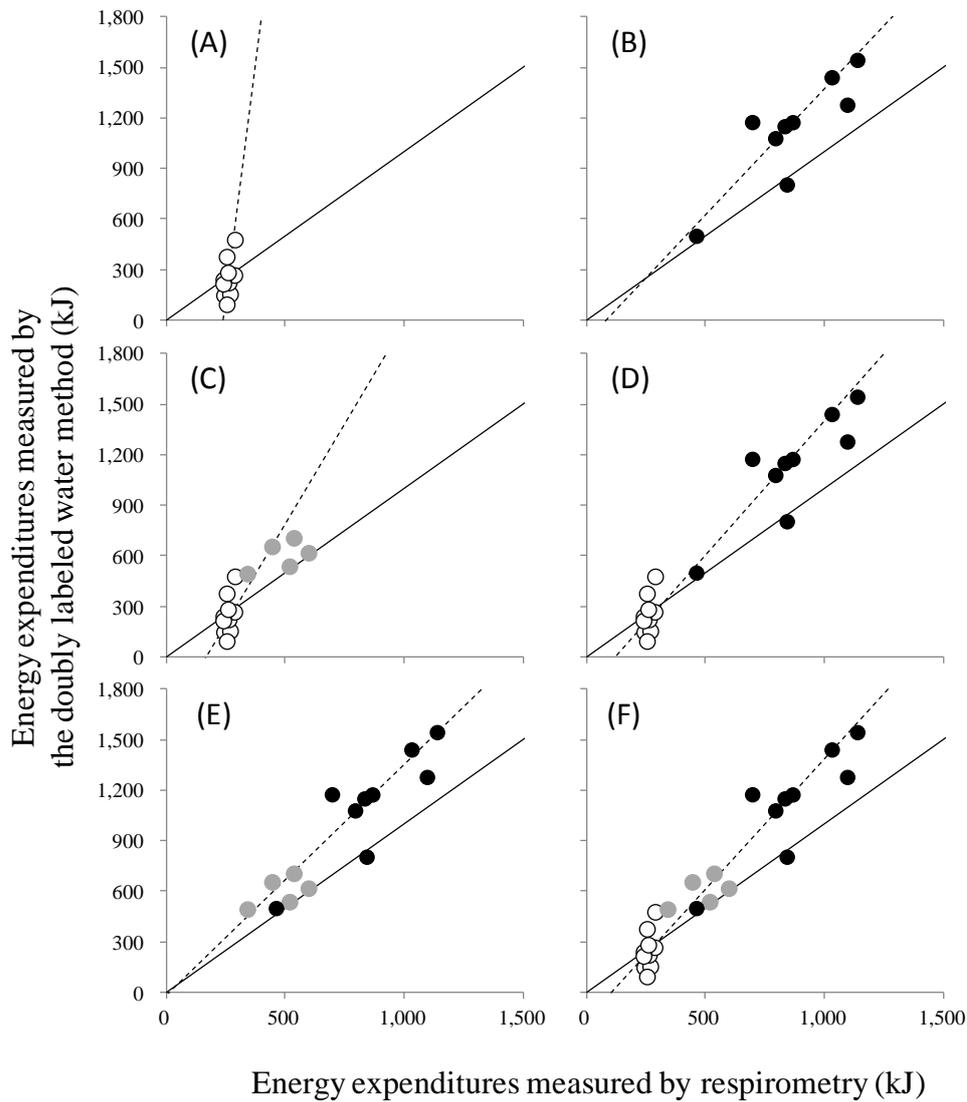


Figure 2.2.

Passing-Bablok regression derived from total energy expenditure in streaked shearwater measured by the doubly labeled water (DLW) method and respirometry using individuals of Group A, B and C (see Materials and Methods). (A) Using Group A; (B) using Group C; (C) using Group A and B; (D) using Group A and C; (E) using Group B and C; (F) using Group A, B and C. White, grey and black circles represent the resulting estimates of Group A, B and C, respectively. The black dashed line and solid line indicates the Passing–Bablok regression line and the line of identity, respectively.

Table 2.1 Metabolic rates, isotope turnover rates and water efflux rate of streaked shearwaters on the ground or on the water. TEE_{resp} and RMR_{resp} represents total energy expenditure and resting metabolic rate measured using the respirometry, respectively. k_d and k_o represents the isotope turnover rate for ^2H and ^{18}O determined using the two-sample technique, respectively. Water efflux rate was calculated from hydrogen isotope turnover rate. Analyses among groups were performed by ANOVA with post-hoc Tukey's HSD multiple comparison test. Different superscripts identify means that differ significantly from each other ($P < 0.05$).

	Group A		Group B		Group C		Statistics	
	Mean	SD	Mean	SD	Mean	SD	<i>F</i>	<i>P</i>
Number of individuals	10		5		9			
Experimental condition	GROUND		GROUND		WATER			
Measurement duration (h)	24.4	0.2	48.1	0.1	24.3	0.3		
Initial body mass (g)	537	38	533	54	559	72	0.51	0.61
Final body mass (g)	503	39	485	50	539	75	1.70	0.21
TEE_{resp} (kJ)	258.6 ^A	17.4	486.4 ^B	98.4	860.9 ^C	210.2	46.03	< 0.001
RMR_{resp} (kJ·g ⁻¹ ·h ⁻¹)	0.0155 ^A	0.0022	0.0153 ^A	0.0021	0.0519 ^B	0.0113	72.77	< 0.001
Isotope turnover rate								
k_d (day ⁻¹)	0.0639 ^A	0.0564	0.0407 ^A	0.0096	0.4248 ^B	0.2257	18.43	< 0.001
k_o (day ⁻¹)	0.1218 ^A	0.0500	0.0981 ^A	0.0123	0.6527 ^B	0.2703	28.25	< 0.001
k_d/k_o	0.4536	0.2699	0.4101	0.0532	0.6192	0.0992	2.67	0.09
Water efflux rate (ml·day ⁻¹)	27.84 ^A	15.81	27.91 ^A	3.84	111.31 ^B	48.66	19.36	< 0.001

Table 2.2 Comparison of total energy expenditures measured by the DLW method (TEE_{dlw}) and respirometry (TEE_{resp}) in streaked shearwaters. TEE_{dlw} were calculated from the five equations from the foregoing studies below. Estimate and ratio represents TEE_{dlw} value calculated using each equation and the ratio between TEE_{dlw} and TEE_{resp} , respectively.

Equations*	Group A		Group B		Group C	
	Mean	SD	Mean	SD	Mean	SD
Experimental condition	GROUND		GROUND		WATER	
Measurement duration (h)	24.4	0.2	48.1	0.1	24.3	0.3
TEE_{resp} (kJ)	258.6	17.4	486.4	98.4	860.9	210.2
TEE_{dlw} (kJ)						
SNG93 (T)						
estimate	248.3	113.2	602.9	86.4	1128.4	316.3
ratio	0.952	0.398	1.267	0.216	1.308	0.212
SP93 (T)						
estimate	253.4	111.9	612.1	87.8	1167.3	329.4
ratio	0.971	0.392	1.286	0.217	1.351	0.216
SCH86 (T)						
estimate	252.7	112.0	610.9	87.6	1162.4	327.7
ratio	0.969	0.393	1.283	0.217	1.346	0.215
SP97 (T)						
estimate	264.0	120.0	640.7	91.8	1201.3	337.0
ratio	1.012	0.421	1.346	0.229	1.392	0.225
SP97 (O)						
estimate	271.4	112.5	645.6	94.4	1279.1	367.2
ratio	1.041	0.393	1.355	0.227	1.477	0.230

*Five equations were used to calculate metabolic rate: SCH86, equation 6 from Schoeller et al. (1986); SP93, equation 4 from Speakman (1993); SNG93, equation 3 from Speakman et al. (1993); SP97, equation 7.17 and 7.43 from Speakman (1997). T and O in parenthesis indicates the two- and one-pool model, respectively.

Table 2.3 Verifications by Passing-Bablok regression analysis for fixed error and proportional error against the respirometry criterion in streaked shearwaters.

No.	Dataset*	Intercept	95% CI for intercept**	Fixed error**	Slope	95% CI for slope**	Proportional error**	Coefficient of determination
1	Group B + C	-14.12	-362.77 to 172.84	Non-Existence	1.37	1.04 to 1.79	Existence	0.82
2	Group C	-119.48	-985.99 to 486.82	Non-Existence	1.50	0.80 to 2.50	Non-Existence	0.65
3	Group A + B + C	-130.28	-311.49 to -36.67	Existence	1.52	1.32 to 1.81	Existence	0.91
4	Group A + C	-195.19	-343.81 to -86.63	Existence	1.60	1.37 to 1.87	Existence	0.91
5	Group A + B	-398.47	-1274.59 to -120.16	Existence	2.38	1.41 to 5.41	Existence	0.27
6***	Group A	-2650.18	N/A	N/A	11.17	N/A	N/A	N/A

* Subjects in three groups were exposed with different experimental conditions: at rest on the ground for 24-hour (Group A) or for 48-hour (Group B), and at rest on the water for 24-hour (Group C).

** Values are the 95% CI for fixed error (intercept \neq 0) and proportional error (slope \neq 1) for each method against the respirometry criterion.

*** Passing-Bablok regression analysis gave false values on 95% CI for intercept and slope and could not evaluate the fix and proportional error.

2.7. Appendices

Table S2.1 Details of all experimental trails. TEE_{resp} is total metabolic rate as measured by respirometry.

Experiment ID	Year	Experimental condition	Measurement duration (h)	Initial body mass (g)	Final body mass (g)	TEE_{resp} (kJ)
A1	2010	GROUND	24.22	482	447	242.2
A2	2010	GROUND	24.22	558	499	267.2
A3	2010	GROUND	24.40	552	519	261.4
A4	2010	GROUND	24.30	538	513	253.1
A5	2010	GROUND	24.48	560	535	285.2
A6	2010	GROUND	24.48	560	535	287.5
A7	2010	GROUND	24.27	580	528	253.0
A8	2010	GROUND	24.47	506	459	239.2
A9	2010	GROUND	24.73	467	447	238.7
A10	2010	GROUND	24.43	562	549	258.6
B1	2013	GROUND	48.02	485	451	516.8
B2	2013	GROUND	48.07	466	415	339.8
B3	2013	GROUND	48.07	560	505	534.9
B4	2013	GROUND	48.33	577	531	596.7
B5	2013	GROUND	48.13	580	523	443.7
C1	2012	WATER	24.08	652	605	792.7
C2	2012	WATER	24.28	670	660	1137.0
C3	2012	WATER	24.38	507	473	840.9
C4	2012	WATER	24.15	530	503	865.0
C5	2012	WATER	24.37	611	600	1029.9
C6	2013	WATER	24.55	553	550	1094.8
C7	2013	WATER	24.12	465	447	460.1
C8	2013	WATER	24.60	563	560	832.0
C9	2013	WATER	23.78	483	454	695.4

Table S2.2 The details of isotope turnover rates (hydrogen, k_d and oxygen, k_o), dilution spaces (hydrogen, N_d and oxygen, N_o) and water efflux rate. k_d/k_o and N_d/N_o is the ratio of the turnover and dilution space of the two isotope labels, respectively. Water efflux rate was calculated from hydrogen isotope turnover rate.

Experiment ID	Experimental condition	Measurement duration (h)	Background enrichment		Initial enrichment		Final enrichment		k_d	k_o	k_d/k_o	N_d	N_o	N_d/N_o	Water efflux rate
			(^2H ; ppm)	(^{18}O ; ppm)	(^2H ; ppm)	(^{18}O ; ppm)	(^2H ; ppm)	(^{18}O ; ppm)	(day^{-1})	(day^{-1})		(mol)	(mol)		(ml day^{-1})
A1	GROUND	24.22	149.8	2006.4	707.7	2998.9	647.0	2852.6	0.1141	0.1580	0.722	15.4	15.6	0.985	33.47
A2	GROUND	24.22	149.8	2006.4	649.6	2894.8	561.1	2704.2	0.1931	0.2394	0.807	16.8	17.1	0.984	62.11
A3	GROUND	24.40	149.8	2006.4	625.4	2875.2	591.9	2771.1	0.0719	0.1255	0.573	17.9	17.7	1.012	27.49
A4	GROUND	24.30	149.8	2006.4	643.9	2913.0	605.7	2821.5	0.0795	0.1050	0.757	17.3	17.0	1.016	25.13
A5	GROUND	24.48	149.8	2006.4	592.8	2840.0	592.6	2792.6	0.0003	0.0574	0.006	19.1	18.3	1.043	11.28
A6	GROUND	24.48	149.8	2006.4	559.4	2796.6	551.9	2709.6	0.0182	0.1144	0.159	20.7	19.3	1.069	20.61
A7	GROUND	24.27	149.8	2006.4	601.4	2862.2	579.9	2754.3	0.0483	0.1333	0.362	19.2	18.3	1.050	38.30
A8	GROUND	24.47	149.8	2006.4	622.8	2883.3	597.3	2788.8	0.0545	0.1119	0.487	18.2	17.7	1.027	35.90
A9	GROUND	24.73	149.8	2006.4	660.2	2949.7	638.6	2861.9	0.0421	0.0948	0.444	16.9	16.5	1.024	16.22
A10	GROUND	24.43	149.8	2006.4	600.2	2851.5	592.5	2787.0	0.0170	0.0780	0.218	18.9	18.2	1.039	7.85
B1	GROUND	48.02	153.9	1998.2	598.4	2984.5	562.3	2805.3	0.0423	0.1002	0.422	20.4	19.2	1.062	22.28
B2	GROUND	48.07	153.9	1998.2	593.9	2976.5	565.7	2819.5	0.0331	0.0873	0.378	20.3	19.0	1.064	26.59
B3	GROUND	48.07	153.9	1998.2	528.7	2824.4	494.0	2656.5	0.0486	0.1134	0.428	24.2	22.9	1.054	32.59
B4	GROUND	48.33	153.9	1998.2	516.2	2794.3	481.0	2642.0	0.0507	0.1054	0.481	24.8	23.6	1.051	29.82
B5	GROUND	48.13	153.9	1998.2	507.2	2770.9	487.5	2651.1	0.0286	0.0840	0.341	25.8	24.7	1.046	28.24
C1	WATER	24.08	146.6	1993.5	518.3	2768.5	457.4	2525.7	0.1784	0.3744	0.477	23.4	23.7	0.988	65.64
C2	WATER	24.28	146.6	1993.5	467.5	2662.5	370.1	2345.9	0.3575	0.6337	0.564	23.3	23.6	0.988	86.70
C3	WATER	24.38	146.6	1993.5	534.9	2797.3	430.4	2487.4	0.3087	0.4792	0.644	20.5	20.9	0.981	86.55
C4	WATER	24.15	146.6	1993.5	594.2	2927.6	360.7	2331.5	0.7330	1.0101	0.726	19.3	19.5	0.989	171.92
C5	WATER	24.37	146.6	1993.5	551.8	2851.3	361.6	2332.9	0.6242	0.9131	0.684	21.8	21.7	1.003	154.66
C6	WATER	24.55	153.9	1998.2	548.8	2867.7	349.1	2330.9	0.6889	0.9392	0.733	23.2	22.0	1.053	174.41
C7	WATER	24.12	153.9	1998.2	626.8	3041.4	571.7	2821.2	0.1231	0.2360	0.522	19.3	18.3	1.055	40.83
C8	WATER	24.60	153.9	1998.2	558.8	2873.3	388.6	2401.1	0.5319	0.7567	0.703	22.5	21.8	1.034	134.32
C9	WATER	23.78	153.9	1998.2	589.6	2959.2	485.0	2565.4	0.2771	0.5321	0.521	20.6	19.5	1.055	86.73

Table S2.3 Comparison of total metabolic rates measured by the DLW method (TEE_{dlw}) and respirometry (TEE_{resp}). Estimate and ratio represents TEE_{dlw} value calculated using each equation and the ratio between TEE_{dlw} and TEE_{resp} , respectively.

Experiment ID	TEE_{resp} (kJ)	SP97 One-pool*		SP97 Two-pool*		SCH86 Two-pool*		SP93 Two-pool*		SNG93 Two-pool*	
		estimate (kJ)	ratio	estimate (kJ)	ratio	estimate (kJ)	ratio	estimate (kJ)	ratio	estimate (kJ)	ratio
A1	242.2	174.5	0.720	157.8	0.652	154.2	0.637	155.1	0.640	148.0	0.611
A2	267.2	193.2	0.723	165.4	0.619	165.5	0.620	167.0	0.625	154.7	0.579
A3	261.4	248.3	0.950	236.8	0.906	227.6	0.871	228.3	0.874	222.7	0.852
A4	253.1	111.4	0.440	100.5	0.397	99.0	0.391	99.6	0.394	94.2	0.372
A5	285.2	282.3	0.990	284.2	0.997	268.8	0.942	269.0	0.943	267.8	0.939
A6	287.5	500.7	1.742	507.9	1.767	481.3	1.674	481.8	1.676	478.3	1.664
A7	253.0	402.9	1.592	400.6	1.583	381.3	1.507	382.0	1.510	377.1	1.490
A8	239.2	263.9	1.103	256.5	1.072	245.3	1.026	245.9	1.028	241.3	1.009
A9	238.7	235.3	0.986	229.4	0.961	219.0	0.918	219.5	0.920	215.9	0.905
A10	258.6	301.3	1.165	300.6	1.163	285.2	1.103	285.5	1.104	283.1	1.095
B1	516.8	575.1	1.113	572.2	1.107	545.8	1.056	546.9	1.058	538.4	1.042
B2	339.8	525.5	1.546	525.3	1.546	500.3	1.472	501.2	1.475	494.4	1.455
B3	534.9	758.1	1.417	751.4	1.405	716.8	1.340	718.3	1.343	707.0	1.322
B4	596.7	668.1	1.120	657.6	1.102	628.7	1.054	630.3	1.056	618.6	1.037
B5	443.7	701.1	1.580	696.8	1.570	662.9	1.494	664.0	1.497	655.9	1.478
C1	792.7	1202.6	1.517	1148.2	1.449	1097.6	1.385	1100.2	1.388	1080.4	1.363
C2	1137.0	1741.0	1.531	1643.3	1.445	1578.3	1.388	1583.3	1.393	1545.2	1.359
C3	840.9	926.2	1.101	857.3	1.020	828.9	0.986	832.3	0.990	805.4	0.958
C4	865.0	1384.8	1.601	1252.8	1.448	1225.2	1.416	1232.2	1.424	1175.2	1.359
C5	1029.9	1659.6	1.611	1536.1	1.492	1492.2	1.449	1499.3	1.456	1442.2	1.400
C6	1094.8	1466.2	1.339	1364.2	1.246	1336.1	1.220	1344.0	1.228	1279.1	1.168
C7	460.1	542.4	1.179	532.3	1.157	510.0	1.108	511.4	1.111	500.6	1.088
C8	832.0	1314.8	1.580	1227.2	1.475	1195.4	1.437	1201.6	1.444	1151.5	1.384
C9	695.4	1274.1	1.832	1250.5	1.798	1197.9	1.723	1201.2	1.727	1176.0	1.691

* Five equations were used to calculate metabolic rate: SCH86, equation 6 from Schoeller et al. (1986); SP93, equation 4 from Speakman (1993); SNG93, equation 3 from Speakman et al. (1993); SP97, equation 7.17 and 7.43 from Speakman (1997).

Table S2.4 Results of analytical variability on total metabolic rate derived from the DLW method (TEE_{dlw}).
 Upper and lower 95% confidence limits, standard deviation and %CV of TEE_{dlw} were calculated using each individual oxygen and hydrogen isotopes analyzed in duplicate (detailed in Method section).

Experiment ID	TEE_{dlw} * (kJ)	Upper 95% confidence limit	Lower 95% confidence limit	Standard deviation	%CV
A1	148.0	170.6	126.0	39.5	26.62
A2	154.7	173.1	136.0	32.8	21.25
A3	222.7	231.8	213.4	16.3	7.30
A4	94.2	108.0	80.6	24.3	25.72
A5	267.8	294.4	240.6	47.5	17.77
A6	478.3	524.5	431.4	82.3	17.22
A7	377.1	392.1	362.1	26.6	7.05
A8	241.3	255.2	227.6	24.3	10.08
A9	215.9	234.1	197.5	32.4	15.01
A10	283.1	300.3	273.3	23.8	8.31
B1	538.4	547.8	529.1	16.5	3.06
B2	494.4	504.4	484.4	17.7	3.57
B3	707.0	723.4	690.4	29.2	4.14
B4	618.6	663.0	575.2	77.6	12.53
B5	655.9	705.7	605.7	88.4	13.48
C1	1080.4	1140.7	1021.7	105.2	9.73
C2	1545.2	1627.1	1465.7	142.7	9.23
C3	805.4	869.5	743.0	111.8	13.87
C4	1175.2	1215.5	1135.6	70.7	6.01
C5	1442.2	1469.4	1415.1	48.0	3.33
C6	1279.1	1358.4	1198.4	141.4	11.06
C7	500.6	547.4	455.1	81.6	16.29
C8	1151.5	1230.8	1069.5	142.6	12.40
C9	1176.0	1213.1	1139.2	65.4	5.56

*Equation 3 from Speakman et al. (1993) was used to calculate metabolic rates.

Chapter 3:

Behavioral and energetic responses to environmental fluctuations and increased flight cost in breeding streaked shearwaters: effects on mates and chicks

3.1. Introduction

Life-history theory predicts that animals should balance their investment in the current reproduction attempt against future opportunities to reproduce (e.g. Stearns 1992). The balance between self-maintenance and future reproduction is particularly relevant to long-lived species, because a small reduction in adult survival can have a large negative impact on lifetime reproductive success (fixed investment strategy) (Charlesworth 1980). Consequences of the trade-off between current reproduction and adult survival have been studied experimentally by increasing the cost of reproduction to parents by means of “handicapping” them (reviewed in Navarro and González-Solís 2007, Bijleveld and Mullers 2009). Although there is considerable evidence to support the prediction of fixed investment strategy in some seabird species, other studies have suggested that reproductive effort in seabirds can be flexible and adjusted according to increased energy demands (flexible investment strategy).

As an explanation for the equivocal results in seabirds, both their strategies of flexible foraging and fluctuations in food availability may complicate their decisions regarding reproductive investment. Since seabirds live in a stochastic marine environment (e.g. Cairns 1988), they may favor a foraging strategy in which foraging effort is flexible, in order to maintain reproductive performance (e.g. Weimerskirch et al. 2001, 2003, Shaffer et al. 2003). This suggests that experimentally increased costs by means of handicapping such as feather clipping do not necessarily produce a trade-off between self-maintenance and current reproduction. Individuals in good breeding condition may respond flexibly to negative energetic balances to maintain reproductive output (i.e. flexible foraging strategy, but not flexible investment strategy), whereas individuals in conditions of low energy availability over the flexibility of foraging effort may be unable to do so, i.e. they will exhibit fixed or flexible investment strategies

(Figure 3.1). It is therefore important to evaluate the degree of flexibility in foraging strategy in subject species, as well as energy availability in a given year, to study the consequences of the trade-off between reproduction and survival in seabirds.

Although a number of studies have observed changes in foraging and provisioning behavior in parental seabirds in response to experimental increases in flying cost (e.g. Paredes et al. 2005, Bijleveld and Mullers 2009, Weimerskirch et al. 2009, González-Medina et al. 2010), there may be difficulties in interpreting whether these changes in behavior represent an increase in reproductive effort. One way to determine the function of changes in foraging behavior is to evaluate the impact of each activity on energy expenditure and intake during a foraging trip. For instance, flight cost is 2-12 times that of resting metabolic rate (RMR) among seabirds (Costa and Prince 1987, Birt-Friesen et al. 1989, Shaffer et al. 2001). Thus, an increase in the proportion of flight time during foraging trips may increase field metabolic rates (FMR) and reduce reproductive effort in some seabird species, but may not have such an effect in others. The influence on energy expenditure and intake of variation in each activity in subject species may determine how that species allocates time and energy during foraging trips when individuals are in poor breeding condition.

Given the expectation that long-lived species prioritize adult survival over reproductive effort (e.g. Erikstad et al. 1998), I hypothesized that streaked shearwater parents ultimately have a fixed level of reproductive investment, and will reduce effort if the costs associated with reproduction increase beyond their flexible foraging strategy threshold. To test these predictions, I first examined the degree of variation in a series of indices of foraging and reproductive effort (behavioral factors affecting energy intake and expenditure, time and energy allocation during foraging trips, quality of fledglings and mass of adults) in streaked shearwaters over two consecutive years. I then

experimentally increased the flight costs of chick-rearing streaked shearwaters via feather clipping, and examined changes in foraging behavior and reproductive performance of manipulated individuals and their mates in the two subsequent years, as measures of change in parental resource allocation between self-maintenance and current reproduction attempt.

3.2. Materials and Methods

The study was conducted from late August to early November in both 2012 and 2013. This work includes the following data from studies performed in both seasons: 1) foraging experiment using the doubly labeled water (DLW) method; and 2) reproduction experiment with experimental increase in cost of flying for parents. The adults' sexes were determined by their vocalizations: males' calls are higher pitched than females' (Arima et al. 2014).

Foraging experiment

I used the doubly labeled water (DLW) method to measure the field metabolic rate (FMR) of adult streaked shearwaters (Lifson & McClintock 1966, Speakman 1997). Shearwaters captured at night were injected with 1.0 ml of a mixture of DLW. I used DLW mixtures with different enrichments of the two isotopes: 34.32 atom % ^2H and 63.76 atom % ^{18}O in 2012; 39.58 atom % ^2H and 58.54 atom % ^{18}O in 2013. The DLW mixture was injected intra-peritoneally by carefully elevating the skin to avoid damage to the air sacs. To precisely quantify the administered dose, the syringe was weighed before and after the injection using an electronic balance that was accurate to the nearest 0.1 mg (Mettler-Toledo, Columbus, OH, USA) in the field laboratory. After injection, these experimental subjects were kept individually in plastic boxes for two hours. I then

took a 1 ml blood sample from the brachial or tarsal vein as an initial sample, and measured their initial body mass (BM_i), using a Pesola spring scale (Baar, Switzerland) with a scale division of 10 g, although I estimated the mass to the nearest gram. The birds were banded with individually numbered metal bands, fitted with a miniature data-logger (see below) and released back into their nests. After a period of 1–7 d, the experimental subjects were recaptured in their burrows at night. Immediately after recapture, I took a 1 ml blood sample as a final sample and measured final body mass (BM_f). I also captured 18 other adult birds not used in the DLW experiment (nine birds in each of 2012 and 2013) and took 1 ml of blood to determine the natural background isotope abundances in each year. Each blood sample was placed in a heparinized tube. After centrifugation (5 min, 6200 rpm), the serum was transferred to a 0.5 ml plastic screw-cap vial with an O-ring (Asahi Techno Glass Co.) and frozen at $-25\text{ }^\circ\text{C}$ until the isotope analysis was conducted.

All isotope analyses were conducted following the procedures given in Chapter 2. Turnover rates of oxygen and hydrogen isotopes (i.e. k_o and k_d) were calculated according to the two-sample technique (Speakman 1997). Body water pools of oxygen and hydrogen isotopes (N_o and N_d) were estimated using the plateau method (Speakman 1997). Since the two-pool model of Speakman et al. (1993) is most appropriate for the streaked shearwater (Chapter 2), I computed the total body water (TBW) at initial capture and CO_2 production rate ($r\text{CO}_2$, mL day^{-1}) using the two-pool model, as follows:

$$r\text{CO}_2 = \left(\frac{N}{2.078} \right) \times (1.01k_o - 1.0532k_d) - 0.246N(1.01k_o - 1.0532k_d),$$

$$\text{where } N = \frac{(N_o / 1.01) + (N_d / 1.0532)}{2} \cdot \left(\frac{BM_i + BM_f}{2BM_i} \right).$$

I assumed an energy equivalence for $r\text{CO}_2$ of $25.11 \text{ kJ L}^{-1} \text{ CO}_2$ (Gessaman and Nagy 1988), to convert the $r\text{CO}_2$ into FMR. In the Chapter 2, I demonstrated that the DLW method does not always provide accurate estimates of energy expenditure, and that for streaked shearwaters it is necessary to correct an overestimation of metabolic rates of more than 30% in situations with high isotope elimination. I thus adjusted the FMR (in kJ day^{-1}) using the following equation (see Chapter 2):

$$\text{Adjusted FMR} = 0.73 \text{ FMR} + 10.31.$$

In the remainder of this study, I present the adjusted FMR estimate as FMR throughout.

The water influx rate ($r\text{H}_2\text{O}$, ml day^{-1}), which is an approximate measure of prey intake (Gabrielsen et al. 1987), was computed using the elimination rate of hydrogen isotopes from the equation of Bevan et al. (1995b; based on Nagy and Costa 1980), as follows:

$$r\text{H}_2\text{O} = \frac{(N_f - N_i) \cdot \ln[(H_i \cdot N_i)/(H_f \cdot N_f)]}{\ln(N_f / N_i) \cdot t} + [(N_f - N_i)/t]$$

$$\text{where } N_i = 18.002 \cdot \frac{(N_o + N_d / R_{\text{dilspace}})}{2}, \text{ and } N_f = N_i \cdot \left(\frac{BM_f}{BM_i} \right).$$

I converted the water influx rate into food intake rate (g day^{-1}) using the water content of anchovy (70%; Takahashi et al. 2001), which is the streaked shearwaters' main prey (Matsumoto et al. 2012), using the following equation (based on Ostrowski et al. 2002):

$$\text{Food intake rate} = \frac{r\text{H}_2\text{O} - W_{\text{met}}}{0.7}$$

where W_{met} = the metabolic water production (ml day^{-1}), calculated as $0.028 \text{ g H}_2\text{O kJ}^{-1}$ of FMR (Schmidt-Nielsen 1997). The food intake rate was converted into kilojoules using 7 kJ g^{-1} as the energy intake rate (EIR).

Reproduction experiment

A total of 72 pairs, each with one chick, were used for the experiment. Pairs were randomly assigned to one of three treatment groups: control (n = 17 pairs, n = 11 in 2012 and 2013, respectively); male-clipping (n = 11, n = 12 in 2012 and 2013, respectively); and female-clipping (n = 11, n = 10 in 2012 and 2013, respectively).

Parents were captured after their chick had hatched (22–31 August in 2012 and between 24 August and 6 September in 2013). Birds were weighed and individually marked with a metal bands. I then fitted a miniature data-logger (see below) to the birds. Finally, I clipped the tip of each primary feather by 3 cm to increase their flight cost (Figure 3.2). Control birds and the partners of clipped birds were handled in the same way but no feathers were clipped.

I recaptured 23 birds (12 males and 11 females) between 26 September and 20 October 2012 and 15 birds (seven males and eight females) between 25 September and 4 October in 2013. At recapture, all birds were weighed and the data-loggers were recovered. Of the recovered data-loggers, one in 2012 and two in 2013 had recording errors and the data were unusable. I also recovered three of the data-loggers that had been fitted in 2012 in subsequent breeding seasons in 2013 and 2014.

I determined the hatching date of each chick by calibrating wing length (maximum flattened chord measured to the nearest 1 mm with a stopped wing rule) against wing growth in chicks of known age (Appendix 3.1). The chicks were then weighed at around 16:00, using a Pesola spring balance with a scale division of 5 g or 10 g, although I estimated their mass to the nearest gram. These measurements were repeated almost every day until fledging, which occurred at an age of more than 65 days (Appendix 3.1). I defined the age and body mass obtained in the final measurements as the fledging age and body mass of the chicks. Streaked shearwater chicks attain a

maximum body mass of approximately 130% of adult mass in mid-October, after which they lose mass (Oka et al. 2002). To calculate the chicks' growth rate and peak mass, I modeled the data for each individual using the following third degree polynomial equation:

$$\text{Chick body mass} = \alpha \text{ age} + \beta \text{ age}^2 + \gamma \text{ age}^3 + \delta,$$

where α , β , γ and δ are the coefficients of the growth curves (Weimerskirch et al. 2000a). I then calculated the age and mass for the asymptote of the polynomial curve (i.e. peak age and body mass; Figure 3.3). I assumed the growth rate of the chicks to be the slope of the tangential line at 50% of peak mass.

Instruments

I deployed miniature data-loggers on all adult shearwaters (Mk-15 or Mk-19; $16 \times 14 \times 6$ mm; Biotrack. Ltd, UK). The loggers weighed only 2.5 g and were attached to a plastic leg band using a weather-resistant cable-tie. These loggers recorded a single sea-surface temperature (SST) value after 20 min of continuous immersion, and only recorded a new value after a subsequent dry period, followed by immersion for a further 20 min. The Mk-15 also recorded saltwater immersion every 3 sec and logged either the total number of positive tests at 10-min intervals, while the Mk-19 recorded immersion at every change of state, from wet to dry and vice versa, exceeding 6 sec. The Mk-19 thus allows reconstruction of the number of landing and take-off events.

The SST data recorded by the data-loggers deployed on the control birds were used to compare the marine environment between 2012 and 2013. Of the data-loggers successfully recovered and downloaded, four failed to record, so I excluded those data from the SST analysis.

In the early and middle chick-rearing periods, if the adults did not sit on water

for a single period of more than 105 min at night (indicated by the immersion data from the data-logger attached to the bird's leg), this indicates that the bird had most likely returned to the nest (Appendix 3.2). I therefore used the wet/dry data, which was recorded only until each chick was 40 days old, to determine the parental attendance schedule (foraging trip duration, intervals between chick provisioning) for each individual or pair.

Data analysis

All data were analyzed using R version 3.0.1 (R Core Team 2013). I used generalized linear models (GLMs) and generalized linear mixed models (GLMMs) for repeated samples (using, for example, nest ID or individual bird as a random factor). *P* values of less than 0.05 were considered statistically significant.

When the dependent variable was foraging trip duration, provisioning interval or time on water while foraging, GLMs and GLMMs were fitted for a Gamma distribution using the “glm” and “glmmadmb” functions (from the glmmADMB package; Fournier et al. 2012), respectively. When the dependent variable was the number of landings during a foraging trip, I fitted GLMs and GLMMs for a negative binomial distribution using the “glm.nb” (from the MASS package; Ripley et al. 2012) and “glmmadmb” functions, respectively. To compare models with two to three independent variables (e.g. year, sex, and presence or absence of feather clipping), I ranked all candidate models with various combinations of the variables and their interactions using the Akaike information criterion (AIC; Burnham and Anderson 2002). I present the results (coefficients and *P* values) from the best model from each model set.

The relationship between metabolic rate and activity is approximately linear

(Puyau et al. 2002, 2004, Yamada et al. 2013), and activity-specific metabolic rates can be calculated as the slope of the regression of metabolic rate (the dependent variable) on each activity (Rezende et al. 2006). I used time spent on water during a foraging trip as the independent variable. I also calculated time in flight, as total foraging trip duration minus time on water, and fitted this to a regression model for estimating the cost of flight. I plotted FMR against each activity to estimate activity-specific metabolic rates for streaked shearwaters. I tested the significance of the interaction term (year \times activity) with an F test using the “anova” function in R, comparing models with and without the interaction term.

To generate curves of energy intake and cost per trip, I plotted intake and metabolic rates (y) against foraging trip durations (T) for each year. EIR and FMR per unit time were correlated with the frequency of landing on water (see Results), so I correct these parameters using their relationships with landing rates to reduce the impact of variation in individual foraging activity (Figure 3.4). FMR and EIR per trip are expected to increase monotonically initially, but then to decrease with increasing foraging trip duration (Kacelnik 1984, Wimerskirch et al. 2003). I therefore used the following asymptotic function to estimate FMR and EIR:

$$y = a - b \times \exp^{-cT}$$

where a , b , and c are the coefficients of the energetic curves and were estimated using the “nlm” function in R. Since FMR is considered to be zero when trip duration is zero, I defined b as equal to a for the FMR curve.

In the analysis for the reproduction experiment (i.e. foraging trip duration, provisioning intervals, time on water, and number of landings), I first compared the data for control individuals or pairs between 2012 and 2013 to assess inter-annual differences in foraging behavior and reproductive performance. I then compared

between control and clipped pairs within each year to investigate the effects of feather clipping on foraging and reproduction in different marine environments.

3.3. Results

Foraging experiment

In 2012 the birds performed significantly longer foraging trips, in terms of duration, than in 2013 (94.5 ± 45.3 h in 2012 vs. 57.6 ± 33.8 h in 2013; Table 3.1) The duration of a single foraging trip positively influenced body mass change during the trip, but there were no differences in body mass change between years or sexes (Figure 3.5, Table 3.1).

From 16 streaked shearwaters (nine in 2012 and seven in 2013) I obtained reliable estimates of FMR and EIR, calculated from water influx rate (Table 3.2). These individuals showed non-significant differences in initial body mass between years, but the TBW percentage was significantly lower for adults in 2012 than in 2013 (Table 3.1). FMR per unit time was higher in 2013 than in 2012, and decreased with foraging trip duration (Figure 3.6, Table 3.1). The EIR per unit time was not significantly different between years and was not correlated with foraging trip duration, but increased with FMR per unit time ($t_{12} = 4.10$, $P < 0.001$), but at a higher rate in 2013 than in 2012 (year \times FMR: $t_{12} = 2.27$, $P = 0.042$; Figure 3.7).

Increased time on water and in flight resulted in a significantly increased trip-specific FMR (Figure 3.8, Table 3.3). The costs of flight and spending time on the water, which were calculated from the slopes of the relevant GLMs, were $0.0329 \text{ kJ g}^{-1} \text{ h}^{-1}$ and $0.0359 \text{ kJ g}^{-1} \text{ h}^{-1}$, respectively. An increase in the frequency of landings raised the FMR per unit time ($t_{13} = 2.98$, $P = 0.011$), with an inter-annual difference ($t_{13} = 6.38$, $P < 0.001$; Figure 3.9). Similarly, an increase in landing rates

raised the EIR per unit time ($t_{13} = 2.39$, $P = 0.033$), but without an inter-annual difference ($t_{13} = 1.25$, $P = 0.235$; Figure 3.9). The proportions of time spent on water and in flight were not correlated with either FMR or EIR ($P > 0.4$ in all cases).

Since FMR and EIR per unit time were correlated with the frequency of landings (Figure 3.9), I corrected these measures using the mean landing frequency (4.0 per hour) for generating energetic curves (see also Figure 3.4). The shapes of the fitted curves for 2012 and 2013 were described by the following equations (Figure 3.10):

$$\text{FMR}_{2012} = 1.925 (1 - \exp^{-0.0189 \times T}),$$

$$\text{FMR}_{2013} = 5.712 (1 - \exp^{-0.0084 \times T}),$$

$$\text{EIR}_{2012} = 8.419 - 13.155 \times \exp^{-0.0325 \times T}, \text{ and}$$

$$\text{EIR}_{2013} = 9.160 - 18.675 \times \exp^{-0.0463 \times T},$$

where T is foraging trip duration in hours. The rate of net gain (i.e. EIR minus FMR), net energy intake per trip, and energy efficiency (i.e. EIR per FMR) were calculated from the curvilinear models (Figure 3.11). Shorter foraging trips yielded a higher rate of net energy gain in 2013 than in 2012, while energy efficiency was higher throughout the 2012 study period than in 2013. Total energy gain per trip was maximized faster in 2013 than in 2012 (Figure 3.11).

Reproduction experiment

Sea surface temperature

The SST recorded by the control individuals during foraging trips differed significantly between years and with foraging trip duration (Figure 3.12, Table 3.4). Shearwaters experienced lower SSTs when they made longer foraging trips and higher SSTs in 2012 than in 2013.

Adult mass

Initial body mass differed significantly between the sexes (597 ± 50 g for males vs. 506 ± 38 g for females; $F_{1,131} = 146.4$, $P < 0.0001$), but there was no difference between years ($F_{1,131} = 0.02$, $P = 0.88$) or among treatments ($F_{2,131} = 0.13$, $P = 0.88$). The amount of body mass change during the experimental period did not differ between years ($F_{1,94} = 0.74$, $P = 0.39$), between sexes ($F_{1,94} = 0.05$, $P = 0.82$) or among treatments ($F_{2,94} = 0.14$, $P = 0.87$).

Year effect on foraging and reproductive behaviors

Control individuals in 2013 performed significantly shorter foraging trips and provisioning intervals than those in 2012 (Table 3.5). Total time on water while foraging was correlated with foraging trip duration, was greater in 2013 than in 2012, and was longer on average for females than for males. The total number of landings was also correlated with foraging trip duration and larger in 2013 than in 2012, and landings were more frequent for females than for males (Table 3.5).

Effects of feather clipping on foraging and reproductive behaviors

None of the variables concerning foraging trips or chick provisioning for individuals in 2012 were affected by feather clipping, whereas clipped individuals in 2013 performed significantly longer foraging trips (Table 3.6). Chick provisioning intervals were however not different among treatments in 2013.

The total time on water in 2012 was correlated with foraging trip duration, and was shorter for males than females (Table 3.6). In 2013, clipped individuals reduced the time spent on water during foraging compared with control individuals. In 2012, the

total number of landings was correlated with foraging trip duration, was less frequent in males than females, and in the partner individuals than control individuals (Table 3.6). Individuals in 2013 did not show any significant effects of feather clipping or sex on the number of landings during foraging trips (Table 3.6).

Chick growth and reproductive success

Fledging success was significantly higher in 2013 than in 2012 ($F_{1,44} = 7.09$, $P = 0.010$), but there was no treatment effect ($F_{2,44} = 0.28$, $P = 0.75$; Figure 3.13, Table 3.7). Although the chicks' growth rate did not differ between years ($F_{1,44} = 0.55$, $P = 0.46$) or among treatments ($F_{2,44} = 0.39$, $P = 0.68$), peak body masses were significantly greater in 2013 than in 2012 ($F_{1,44} = 15.18$, $P = 0.0003$) but did not differ not among treatments ($F_{2,44} = 0.09$, $P = 0.92$; Figure 3.13, Table 3.7).

Fledging mass, and age at peak mass and at fledging showed significant effects of the interaction between year and treatment (fledging mass: $F_{2,44} = 6.98$, $P = 0.002$; age at peak mass: $F_{2,44} = 5.13$, $P = 0.01$; age at fledging: $F_{2,44} = 5.95$, $P = 0.005$). In the control groups, there was no difference between the years for any of these chick-related measures ($P > 0.3$ in all cases). Similarly, there was no difference between the control and treatment groups in 2013 for any of these chick-related measures ($P > 0.2$ in all cases). However, in 2012, chicks from the male-clipped pairs had lower body mass at fledging ($t_{19} = 3.47$, $P = 0.0026$) and attained their peak mass ($t_{19} = 2.38$, $P = 0.028$) and fledged ($t_{19} = 3.70$, $P = 0.0015$) more quickly than those in the control group. There was not, however, any difference between the chicks from control and female-clipped pairs ($P > 0.1$ in all cases).

3.4. Discussion

Foraging experiment

Activity-specific metabolic rates

My results show that the cost of flight for streaked shearwaters (2.0 times RMR on the ground, which is $0.0154 \text{ kJ g}^{-1} \text{ h}^{-1}$; Chapter 2) was approximately equal to the cost of sitting on water (2.3 times RMR). Their estimated cost of flight is similar to that of albatrosses (2-4 times RMR), which have one of the lowest costs of flight among seabirds (Costa and Prince, 1987, Shaffer et al., 2001, 2004). This low flight cost may be the result of their use of dynamic soaring flight (Sato et al. 2009) and low flight altitude (1 m above sea level; Ueta et al. 2011), which takes advantage of the ground effect (Withers and Timko 1977, Richardson 2011). Streaked shearwaters are known to perform wide-ranging foraging trips, traveling more than several hundred kilometers from their breeding site (Yamamoto et al. 2012, Ito et al. 2013), and this low flight cost may be what makes it possible for them to undergo such long-distance movements.

In contrast, of those foraging behaviors that I measured, the one most closely associated with field metabolic rate (FMR) and energy intake rate (EIR) was the rate of landings and take-offs (Figure 3.9). This indicates that landings and take-offs, accompanied by flapping flight (Sato et al. 2009), are energetically expensive for streaked shearwaters. Because of their long, narrow wings (Shirai et al. 2013), flapping flight may require a high physical power output (Alerstam et al. 1993). My results suggest particularly strong morphological trade-offs for streaked shearwaters, which use their wings for wide-ranging flight and landing for feeding.

Flexible foraging strategy

As with other procellariiform seabirds (reviewed in Baduini and Hyrenbach

2003), trip duration for streaked shearwaters varies widely, from one to more than 10 days (Ochi et al. 2010). My results showed that streaked shearwaters rearing chicks are faced with a trade-off between shorter foraging journeys to maximize the net gain rate (i.e. the rate of chick provisioning), and longer foraging to increase parental body reserves by increasing net energy intake (Figures 3.5 and 3.11). Foraging animals have to adjust their foraging effort in relation to time and energy constraints (Ydenberg and Hurd 1998). Chick-rearing birds face the constraint of time, with respect to chick provisioning (Stephens and Krebs 1986). To shorten the provisioning interval while maintaining net energy intake, parental birds may increase their energy expenditure rate and net gain rate, although this would decrease the energy efficiency of their foraging trips (Ydenberg 1994, Ydenberg and Hurd 1998; Figure 1.2). In streaked shearwaters, the longer the foraging trip, the lower their FMR was (Figure 3.6). As with previous results for blue petrels *Halobaena caerulea* (Weimerskirch et al. 2003), my results indicate that streaked shearwaters can make a compromise by alternating the foraging currencies between shorter and longer trips, which may be beneficial for both chick growth and self-maintenance.

With respect to the relationship between EIR and FMR between the years, an increase in FMR contributed to an increase in EIR in both years, but this rate was significantly lower in 2012 than in 2013 (Figure 3.7). This suggests that foraging conditions in 2012 were such that it was difficult to increase energy acquisition by increasing foraging effort. When the streaked shearwaters experienced poorer foraging conditions, they significantly decreased their FMR (Table 3.1), as with little auks (Welcker et al. 2009b) and black-legged kittiwakes (Jodice et al. 2006). As a consequence, the birds in 2012 experienced a lower rate of net gain on shorter foraging trips, while they showed a higher energy efficiency than those in 2013 (Figure 3.11).

The foraging currencies to be maximized may differ according to whether animals are self-feeding (i.e. energy efficiency) or provisioning offspring (i.e. net rate of gain; e.g. Ydenberg et al. 1994, Ydenberg and Hurd 1998; Figure 1.2). My results, thus, suggest that parents in poorer energy availability conditions modify their foraging trips to decrease the burden of self-maintenance by reducing their FMR. The difference in FMR between years may also reflect either or both behavioral change or/and intrinsic physiological changes. Although the birds whose FMR I measured did not show inter-annual differences in any foraging behaviors, including the proportion of time in flight and on water, and the frequency of landings (Figure 3.9), I did observe a lower percentage of TBW in 2012 (Table 3.1), which may be linked to an increase in lipid content (Niizuma 2011, Jacobs et al. 2012). Lipids generally have lower metabolic rates compared with other body tissues such as muscle (Scott and Evans 1992). Thus, increased body lipids may have contributed to reducing the birds' basal metabolism in 2012. My hypothesis that the shearwaters' inter-annual differences in FMR were at least partially related to intrinsic physiological changes therefore seems more likely to be correct. Overall, my results indicated that streaked shearwaters can flexibly modify their foraging effort within and between years.

Reproduction experiment

Inter-annual adjustments in reproductive performance in relation to environmental changes

Streaked shearwaters experienced significantly different SSTs in the two years of this study (warmer in 2012 and cooler in 2013; Figure 3.12), and this inter-annual difference in SST presumably influenced the difference in energy availability between the years (Figure 3.7). Indeed, in the cooler year, birds performed shorter foraging trips

and showed higher provisioning rates than in the warmer year. The chicks also had higher fledging success and peak body mass in 2013 than in 2012, presumably because of the shorter provisioning intervals in 2013. Procellariiformes generally show a high frequency of provisioning when local areas are more productive, presumably to maximize energy delivery to their chicks (e.g. Duriez et al. 2000, Weimerskirch et al. 2001, Einoder et al. 2013). This suggests that the marine environment in 2013 (cooler) was substantially more favorable for streaked shearwaters than that in 2012 (warmer).

Although the breeding conditions in 2012 were probably less favorable for streaked shearwaters, the chicks from control pairs that fledged successfully showed no difference in fledging mass or age between the years (Figure 3.13, Table 3.7). This suggests that the total amount of energy provided by the parents was similar during the chick-rearing period across years. The similar fledging condition but higher peak body mass observed in 2013 implies that parents in that year were able to maintain a higher provisioning rate and left the breeding colony earlier than those in 2012. The control parents in 2012 performed less frequent landings on water per trip (i.e. lower foraging effort) and longer foraging trips (Table 3.5). To compensate for the lower daily energy flow to chicks in 2012, the parents may have been obliged to extend the duration of parental care. This also supports a previous finding that streaked shearwaters may sustain provisioning effort to ensure the optimal amount of reproductive investment (Ogawa et al. 2015). Overall, my inter-annual comparison of reproductive performance suggests that streaked shearwaters maintain their chicks' condition by altering the duration of foraging trips and of parental care in accordance with energy availability.

Effects of feather clipping on parental behavior and chick growth

When challenged by the additional flight cost, the birds showed different

behavioral modifications between years (Figure 3.14). Clipped shearwaters in 2013 (i.e. favorable breeding conditions) performed longer foraging trips and reduced the time they spent on the water compared with the control birds, and their partners did not show any behavioral response (Figure 3.14A, Table 3.6). The growth and condition of the chicks of manipulated pairs were not different with those of control chicks (Figure 3.13). The behavioral responses of clipped individuals corresponded with the birds' general response to unfavorable breeding conditions (increased foraging trip duration and reduced time spent on the water; see above), except for the change in landing frequency, which was important for maintaining their energy intake and expenditure rates (Figure 3.9). Increased foraging trip durations may have contributed to increased net energy intake (Figure 3.11). The decreased time spent on the water indicates an increase in time spent in flight, which would have made it possible to search more actively for productive areas without changing the EIR or FMR (Figure 3.9). This suggests that under favorable breeding conditions clipped individuals could compensate for the additional cost by adjusting their foraging strategy.

The opposite pattern was observed in 2012 (i.e. unfavorable breeding conditions), when the clipped birds showed no behavioral responses, while the partner birds changed their foraging behaviors (reduced the number of landings) compared with the control birds (Figure 3.14B). Foraging trip duration was already greater because of the limited energy availability, and the proportion of time spent on the water and the frequency of landings were lower, in 2012 (Table 3.5). As a result of the additional flight cost, the clipped shearwaters may have faced their threshold of foraging flexibility. The lack of behavioral response in the clipped birds thus suggests that further behavioral modifications would be too costly for survival and subsequent breeding attempts in this long-lived species. The change in the body mass of the parents did not

differ between treatments, although the chicks of the male-clipped pairs had a lower fledging body mass and fledged more quickly (Figure 3. 13, see also below). These results support the prediction that individuals of this long-lived species will prioritize self-maintenance over their current reproductive attempt (Stearns 1992).

However, the partners of the clipped birds did reduce their frequency of landings during foraging trips (Table 3.6). Since the reduced landing rate may have decreased their FMR (Figure 3.9), and the EIR in 2012 was relatively independent of FMR (Figure 3.7), this behavioral change may have resulted in an increased energy intake per foraging trip (Figure 3.14B). The partners of handicapped Antarctic petrels *Thalassoica antarctica* did not change their behavior or lose body mass (Sæther et al. 1993), whereas the partners of handicapped thick-billed murres showed an increase in nest attendance (Paredes et al. 2005). Because procellariiform seabirds generally fly at least several hundred kilometers to their foraging grounds, the partners of handicapped individuals are expected to be limited in their ability to recognize reduced reproductive effort in their mate. However, when both streaked shearwater parents visit the nest, the parent that arrives second recognizes when the chick has received a full meal, because it reduces the amount of food it provides to the chick (Ogawa et al. 2015). That parent then lengthens its next foraging trip. This implies that the partners of the handicapped shearwaters recognized the reduced effort of their mates' nest attendance indirectly. Furthermore, it suggests that the fact that the second-arriving parents have the capacity to provide more food than necessary functions as a form of insurance for when the effort of their mate is reduced.

In 2012, only chicks from male-clipped pairs attained their peak mass more quickly, had a lower fledging mass, and fledged sooner than control chicks (Figure 3.13). This indicates that the male-clipped pairs were unable or unwilling to fully compensate

for the assumed reduction in energy delivery when breeding conditions were unfavorable. Chicks from the female-clipped pairs did not show any significant difference from control chicks. This implies that the sex-related difference in reproductive performance may be the result of either a sexual difference in the impact of feather clipping, or a sexual difference in the capacity to compensate a mate's reduced provisioning. The provisioning interval was not significantly different among treatments in 2012 (Table 3.6). The chicks from male-clipped pairs in 2012 showed similar growth rates and peak body mass to those of the control and female-clipped pairs (Figure 3.7). The total duration of their parental care may therefore have been shorter than the other treatment groups. A previous study suggests that female streaked shearwaters leave the colony and depart from the ocean surrounding the colony for migration earlier than males (Yamamoto et al. 2010). This implies that males and females may have different schedules of parental care, such that males contribute more to chick growth in the late chick-rearing period. Since the negative effects of the experimental manipulation were apparent in the late chick-rearing period (i.e. body mass and age at fledging), but not in the early period (i.e. growth rate and peak body mass), the hypothesis that the impact of feather clipping on reproduction is greater for males than for females, seems likely to be correct.

3.5. Conclusion

My study demonstrates that long-lived seabirds within one population can use both fixed and flexible investment strategies, according to energy availability. Foraging energetics and behavior, nest attendance and experimental manipulation of flight cost suggest that streaked shearwaters have highly flexible foraging strategies. The variation in foraging trip duration results from regulation of shorter and longer foraging trips for

chick provisioning and self-maintenance. When energy availability was high, parents handicapped by feather clipping could maintain both their own and their chick's condition without compensation by their partner, but under lower energy availability, handicapped birds may have been unable to sustain both self-maintenance and reproductive effort. The partners of clipped birds in unfavorable conditions compensated for the reduced reproductive effort, but the degree of compensation may have differed between the sexes. Since the parents in all treatments maintained their body mass on average, my results support the prediction of life-history theory that long-lived animals should limit their risk of increased mortality during a breeding attempt because of the high residual reproductive value (Williams 1966). This highlights the fact that long-lived seabirds have a threshold level of flexibility in their reproduction strategy, and that they support this prediction of life-history theory only when breeding conditions are below the threshold (Stearns 1992, McNamara and Houston 1996).

3.6. Figures and Tables

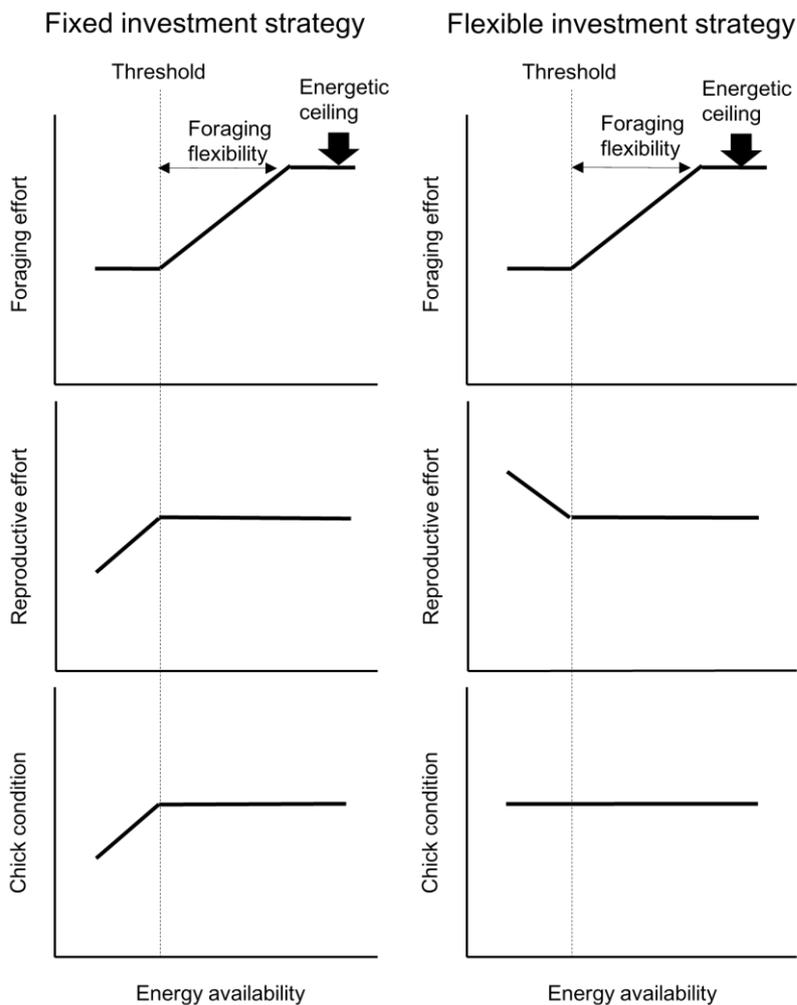


Figure 3.1.

Schematic of study hypotheses. I hypothesized that foraging flexibility in seabirds compensates for decreased energy availability to a certain extent, and provides buffers to prevent negative consequences for both chicks and parents. Only below a certain threshold in foraging flexibility will parents be forced to select either flexible or fixed investment strategies to transfer the cost to themselves or their chicks.



Figure 3.2.

Control or partner (a) and handicapped (b) individuals.

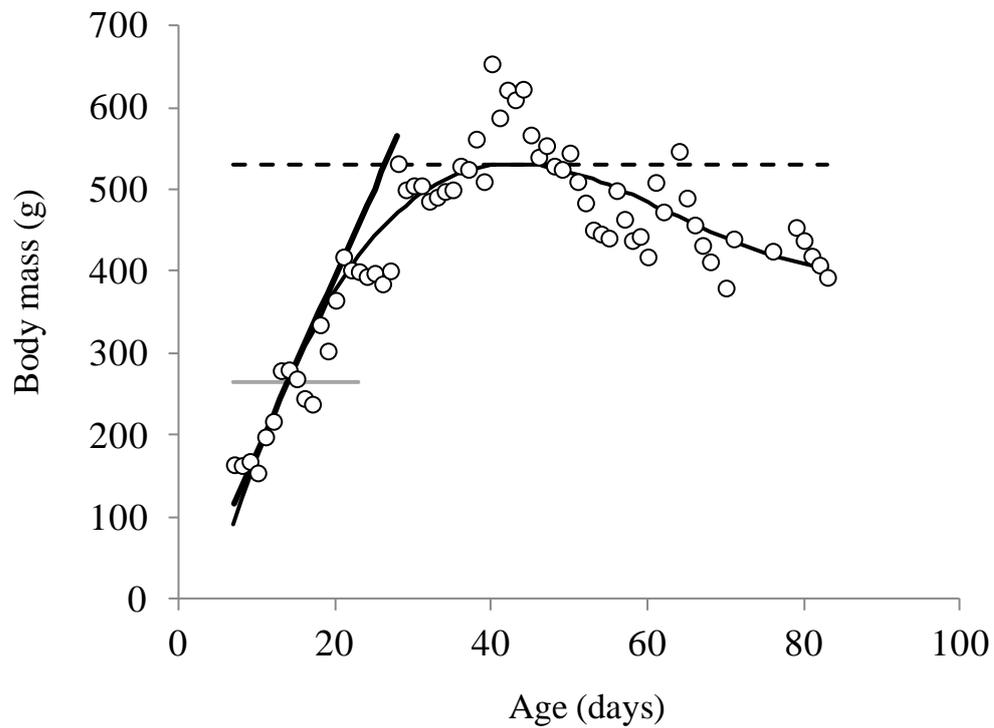


Figure 3.3.

Example of change in mass of a shearwater chick through the chick-rearing period, modeled using a third degree polynomial growth curve (thin black solid line). The black dashed and thin grey lines indicate peak body mass and half of the peak body mass, respectively. The thick black solid line is a tangential line drawn at the half of peak body mass point for this chick, the slope of which was taken to be the growth rate.

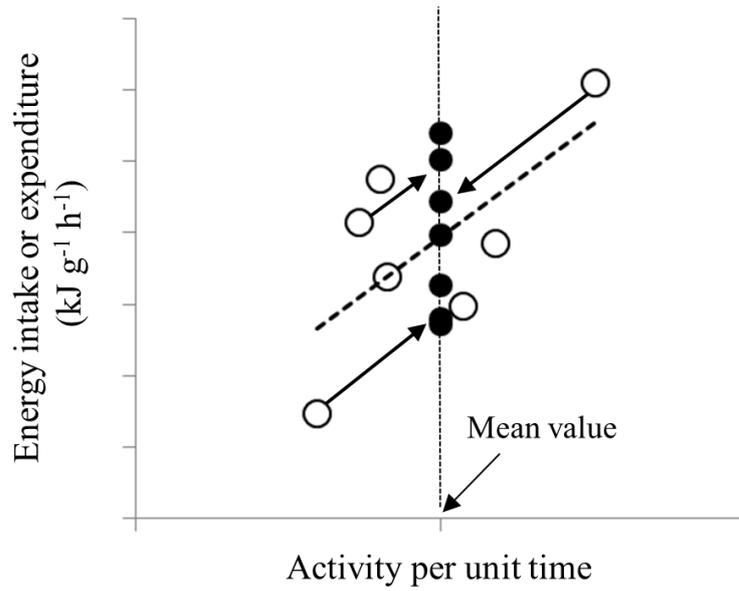


Figure 3.4.

A bivariate plot of field metabolic rate (FMR) (or energy intake rate: EIR) versus activity per unit time. The effects of activity on FMR or EIR are eliminated from each individual based on regression lines (thick dashed line). Data points situated on the regression line are transformed to the points where this line intersects the arithmetic mean of activity per unit time (thin dashed line).

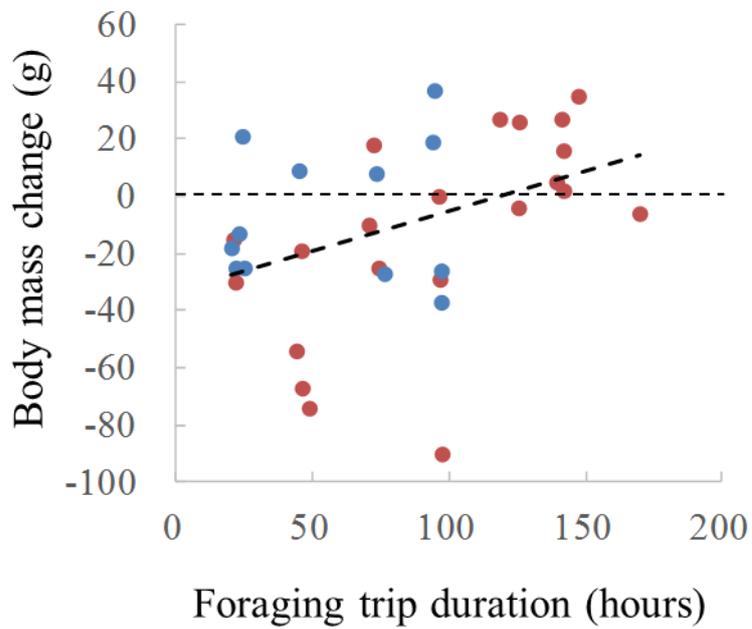


Figure 3.5.

The relationship between body mass and total body water (estimated using isotope dilution) for streaked shearwaters. Red and blue circles indicate individuals in 2012 and 2013, respectively.

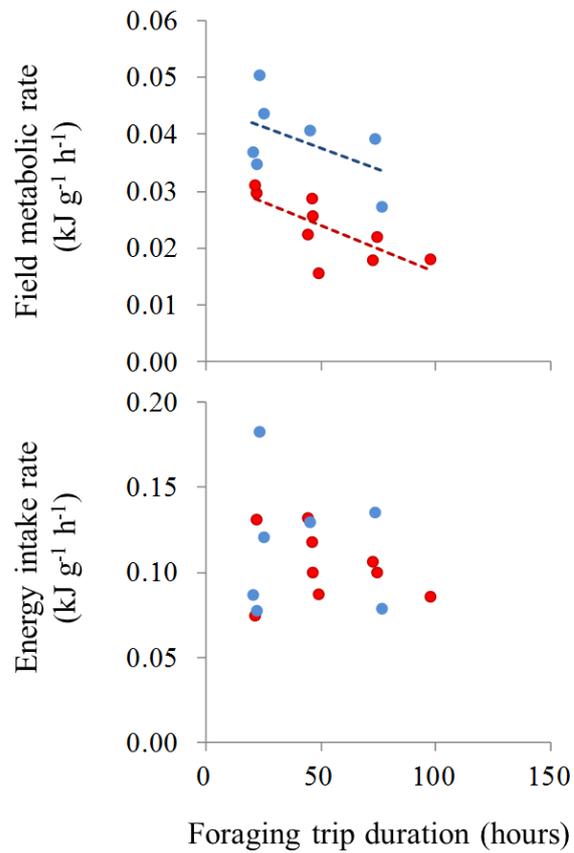


Figure 3.6.

Changes in field metabolic rate and energy intake rate according to foraging trip duration in 2012 (red) and 2013 (blue).

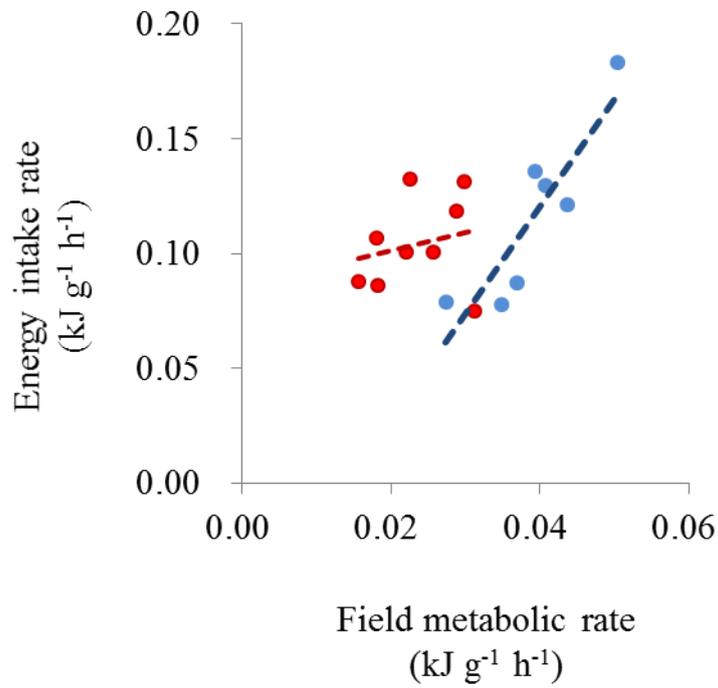


Figure 3.7.

Field metabolic rate in relation to energy intake rate during the chick-rearing period in 2012 (red) and 2013 (blue).

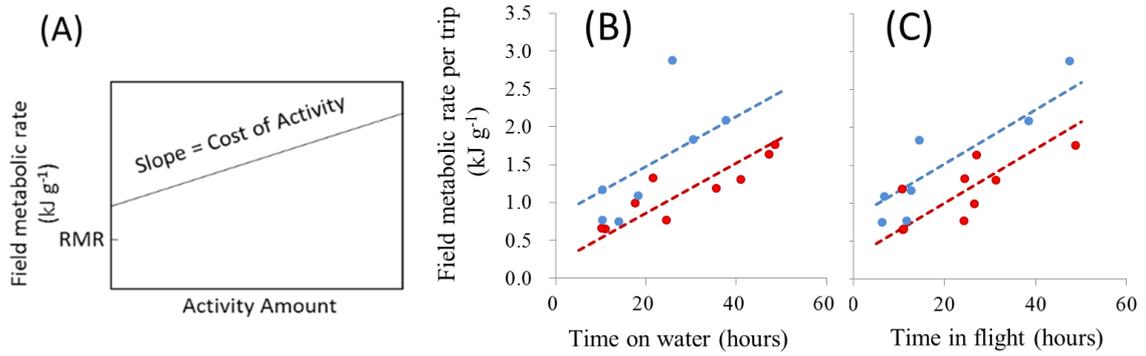


Figure 3.8.

(A) Schematic representation of the calculation of activity cost using the regression shown for FMR per gram against each activity during a foraging trip. The cost of an activity was determined as the slope of the relevant generalized linear model. The data show the relationship between FMR and (B) time on water and (C) time in flight, as recorded by data-loggers attached to the birds' legs.

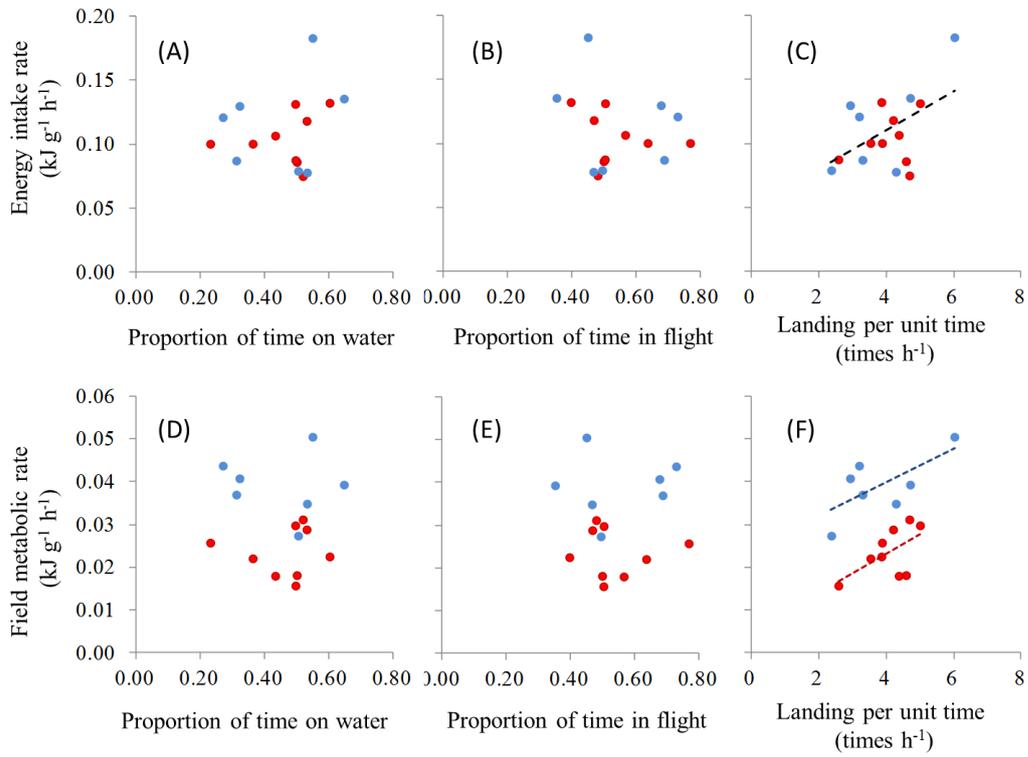


Figure 3.9.

Comparison of correlations between with field metabolic rate or energy intake rate and foraging activity in 2012 (red) and 2013 (blue).

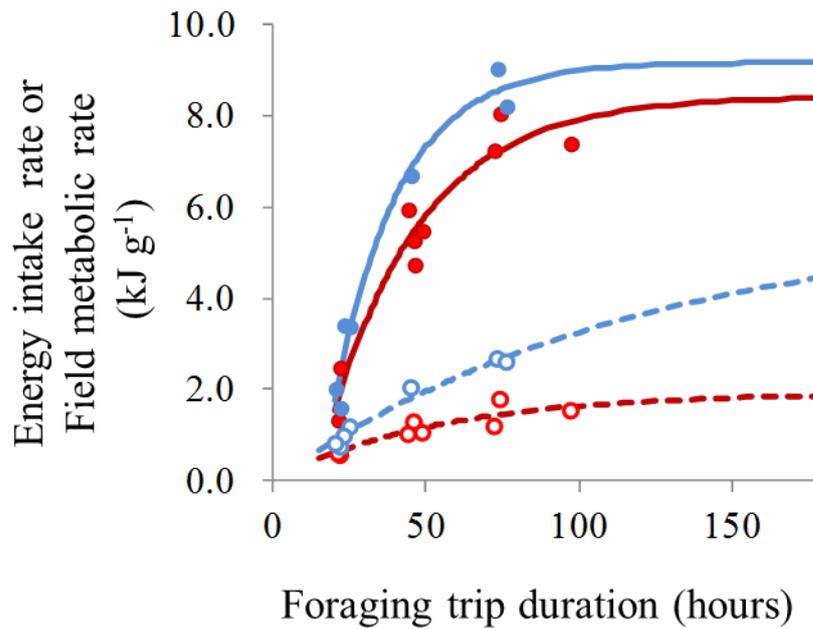


Figure 3.10.

The relationship between energy intake rate (EIR; closed circles) or field metabolic rates (FMR; open circles) (corrected by the frequency of water landings during foraging trips) and foraging trip duration at sea in 2012 (red) and 2013 (blue). The curves are the predicted relationships, indicating that although EIR and FMR increased with increasing foraging trip duration, the rate of increase declined.

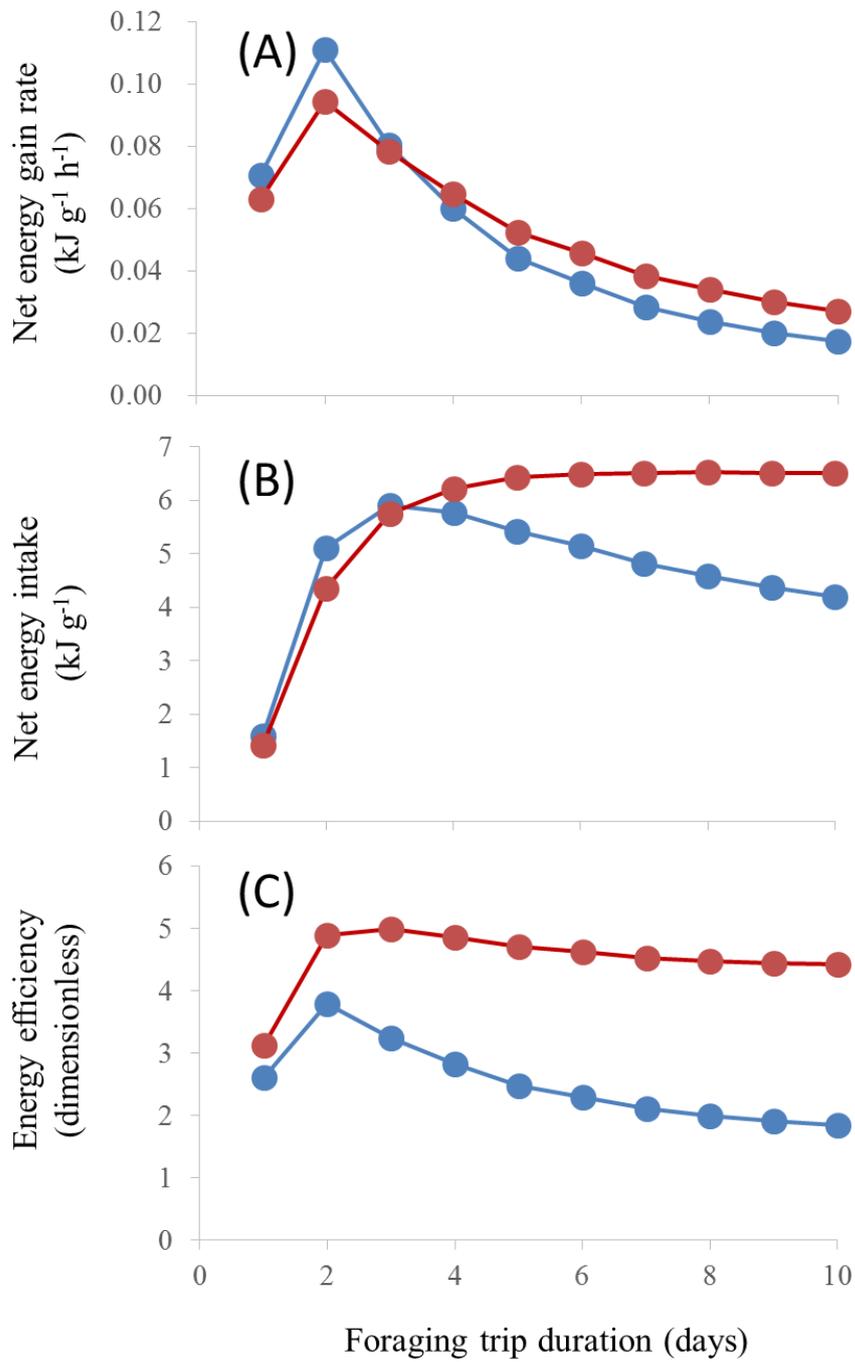


Figure 3.11.

(A) Estimated rate of net gain, (B) net energy intake, and (C) energy efficiency, in relation to foraging trip duration in 2012 (red) and 2013 (blue).

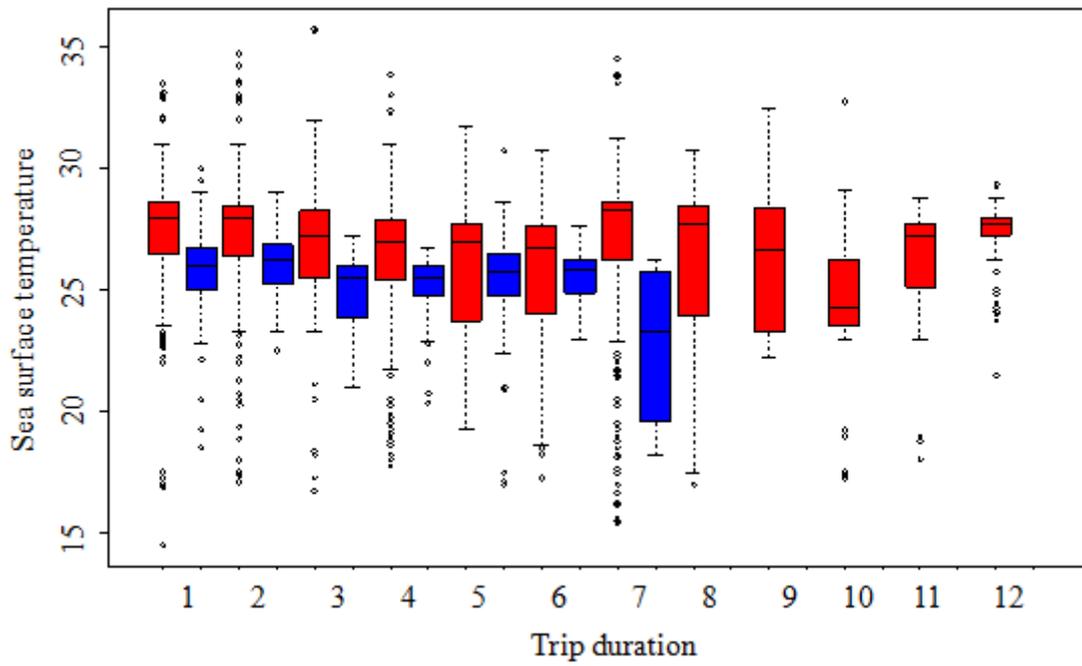


Figure 3.12.

Average sea-surface temperature (± 1 SD) in relation to foraging trip duration, as recorded by animal-borne data-loggers for 2012 (red) and 2013 (blue).

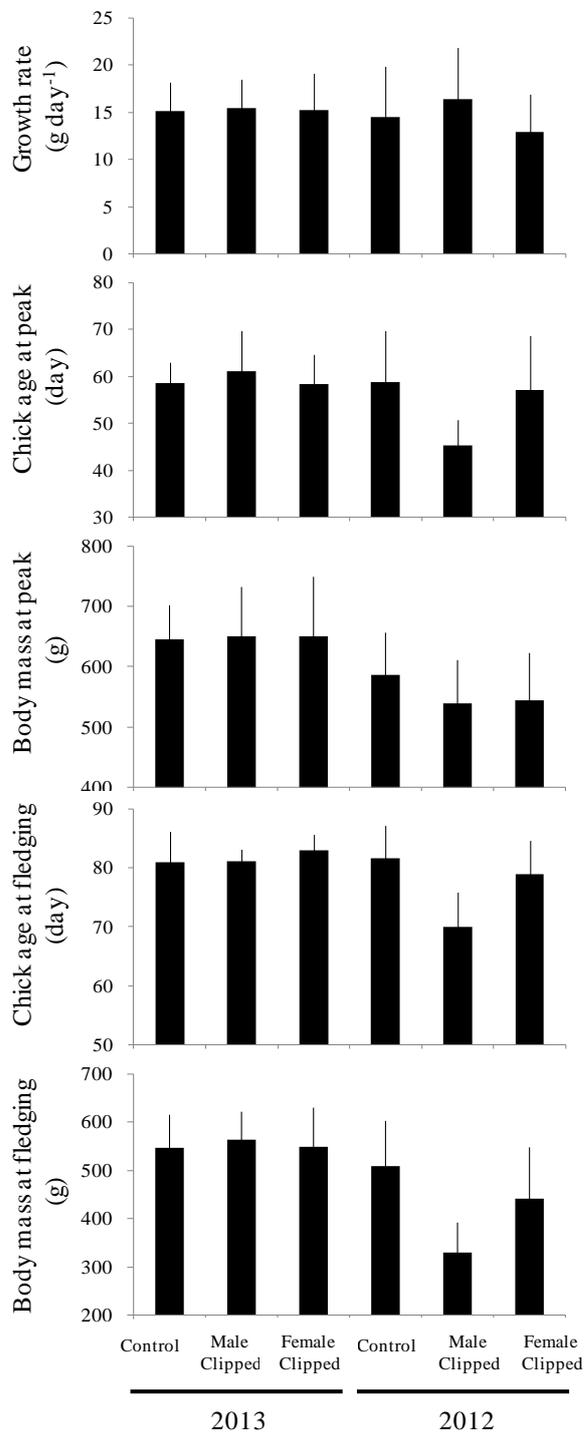


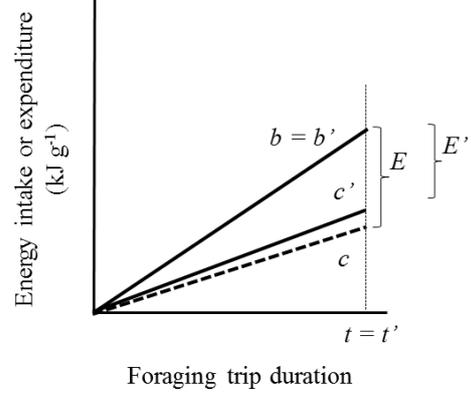
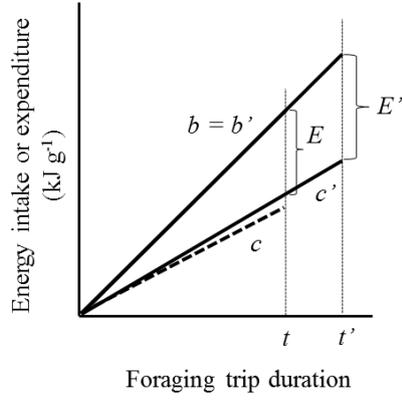
Figure 3.13.

Average (± 1 SD) growth parameters of streaked shearwater chicks for two years.

(A) Favorable conditions

(B) Unfavorable conditions

Clipped birds



Partner of clipped birds

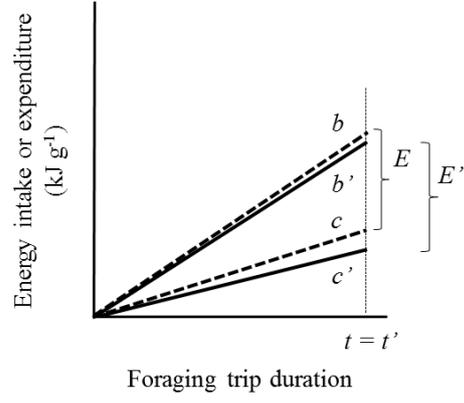
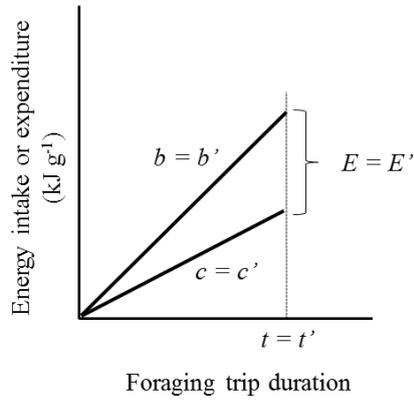


Figure 3.14.

Models of foraging effort that illustrate the relationships between foraging trip duration (t , t') and energy intake (b , b') and expenditure rates (c , c'), and total energy intake (E , E') associated with manipulations (based on Ydenberg et al. 1994). Indices for control individuals in each condition state are represented by t , b , c and E . (A) Under the favorable breeding conditions in 2013, clipped birds, which were forced to increase their energy expenditure ($c' > c$), made longer foraging trips ($t' > t$). As a consequence, total energy intake in the clipped birds may have been similar to that in the control birds ($E' \sim E$). In contrast, the partners of the clipped birds did not show any difference from the control birds. (B) Under the unfavorable breeding conditions in 2012, clipped birds did not change their foraging behavior, and thus the increase in flight cost caused by feather clipping may have reduced their total energy intake ($E' < E$). The partners of the clipped birds reduced the frequency of their landings on water. The frequency of landings is positively correlated with both energy intake and expenditure rates (Figure 3.9). In addition, the rate of energy expenditure has a weak relationship with the rate of energy intake (Figure 3.7). The behavioral change of the partners therefore reduced both their energy intake ($b' < b$) and expenditure rates ($c' < c$), although this effect was larger for intake than expenditure ($b' - b < c' - c$). Thus the partners' total energy intake may have increased slightly ($E' > E$).

Table 3.1 Model (GLM) selective results (displayed are selected models with the lowest AIC) of parental indices for the effects of sex (male or female), year (2012 or 2013) and trip duration in Foraging experiment. Effects on parental indices are measured as trip duration, and body mass change from all injected individuals, and as body mass, total body water, field metabolic rate and energy intake from individuals obtained reliable estimates of field metabolic rates.

Response variable	Best model	Fixed effect	Estimate (\pm SE)	<i>t</i>	<i>P</i>
Trip duration	Year	Intercept	0.0106 (\pm 0.0012)	8.818	<0.001
		Year	0.0068 (\pm 0.0029)	2.361	0.025
Body mass change	Trip duration + Year + Sex	Intercept	-59.11 (\pm 13.79)	-4.287	<0.001
		Trip duration	0.39 (\pm 0.12)	3.349	0.002
		Year: 2013	21.13 (\pm 10.65)	1.984	0.057
		Sex: Male	18.07 (\pm 9.41)	1.921	0.065
Initial body mass	Sex	Intercept	507.8 (\pm 12.5)	40.79	<0.001
		Sex: Male	84.1 (\pm 17.6)	4.779	<0.001
Total body water	Year	Intercept	0.495 (\pm 0.003)	161.7	<0.001
		Year: 2013	0.042 (\pm 0.005)	8.314	<0.001
Field metabolic rate	Trip duration + Year	Intercept	0.0319 (\pm 0.0034)	9.411	<0.001
		Trip duration	-0.00016 (\pm 0.00006)	-2.864	0.013
		Year: 2013	0.0136 (\pm 0.0027)	5.077	<0.001
Energy intake rate	Null	Intercept	0.1095 (\pm 0.0072)	15.17	<0.001

Table 3.2 Indices of metabolism of streaked shearwater during foraging in 2012 and 2013.

	2012		2013	
Number of individuals	9		7	
Sex	Male (n = 4)	Female (n = 5)	Male (n = 3)	Female (n = 4)
Initial body mass (g)	581 ± 26	505 ± 53	611 ± 42	511 ± 18
Total body water (%)	57.1 ± 2.1		65.1 ± 2.2	
Field metabolic rate (kJ g ⁻¹ h ⁻¹)	0.0236 ± 0.0056		0.0391 ± 0.0072	
Energy intake rate (kJ g ⁻¹ h ⁻¹)	0.1042 ± 0.0201		0.1162 ± 0.0381	

Table 3.3 Model (GLM) estimates of field metabolic rate in relation to activity at sea

Activity	Fixed effect	Estimate (\pm SE)	<i>t</i>	<i>P</i>
Flight	Intercept	0.2038 (\pm 0.2864)	0.712	0.489
	Time in flight	0.0329 (\pm 0.0087)	3.790	0.002
	Year: 2013	0.6173 (\pm 0.2268)	2.722	0.017
Contacting with water	Intercept	0.2860 (\pm 0.1872)	1.528	0.150
	Time on water	0.0359 (\pm 0.0063)	5.700	<0.001
	Year: 2013	0.5178 (\pm 0.1704)	3.038	0.010

Table 3.4 Model (GLMM) estimates of sea surface temperature in relation to year and trip duration

	Estimate	<i>z</i>	<i>P</i>
Fixed effects			
Intercept	27.75±0.20	138.06	<0.0001
Year-2013	-0.95±0.25	-3.83	0.0001
Trip duration	-0.26±0.01	-20.72	<0.0001
	<u>Variance</u>		
Random effect			
Individual (intercept)	0.879		

Table 3.5 Model (GLMM) selection results (displayed are selected models with the lowest AIC) of parental behavior for the effects of sex (male or female), year (2012 or 2013) and trip duration in the control groups. Effects on parental behaviors are measured as trip duration, provisioning interval, and time on water and the number of landing during foraging. Effects of trip duration analysed for time on water and the number of landing.

Response variable	Best model	Fixed effect	Estimate (\pm SE)	Z	P
Trip duration	Year	Intercept	0.784 (\pm 0.052)	15.00	<0.0001
		Year: 2013	-0.387 (\pm 0.085)	-4.56	<0.0001
Provisioning interval	Year	Intercept	0.314 (\pm 0.034)	9.23	<0.0001
		Year: 2013	-0.139 (\pm 0.063)	-2.20	0.028
Time on water	Trip duration + Year + Sex + Trip duration \times Year	Intercept	1.966 (\pm 0.056)	35.09	<0.0001
		Trip duration	0.418 (\pm 0.020)	21.06	<0.0001
		Year: 2013	-0.314 (\pm 0.075)	-4.17	<0.0001
		Sex: Male	-0.166 (\pm 0.051)	-3.28	0.001
		Trip duration \times Year: 2013	0.171 (\pm 0.041)	4.17	<0.0001
Number of landing	Trip duration + Year + Sex + Trip duration \times Year	Intercept	4.633 (\pm 0.078)	59.50	<0.0001
		Trip duration	0.381 (\pm 0.023)	16.71	<0.0001
		Year: 2013	0.259 (\pm 0.104)	2.48	0.013
		Sex: Male	-0.189 (\pm 0.094)	-2.01	0.045
		Trip duration \times Year: 2013	0.091 (\pm 0.044)	2.09	0.037

Table 3.6 Model (GLMM) selection results (displayed are selected models with the lowest AIC) of parental behavior for the effects of sex (male or female), treatment (control, clip or partner), group (control, maleclip or femaleclip) and trip duration. Effects on parental behaviors are measured as trip duration, provisioning interval, and time on water and the number of landing during foraging. Effects of group analysed for provisioning interval only. Effects of trip duration analysed for time on water and the number of landing.

Response variable	Best model	Fixed effect	Estimate (\pm SE)	Z	P
2012					
Trip duration	Sex	Intercept	0.828 (\pm 0.062)	13.47	<0.0001
		Sex: Male	-0.135 (\pm 0.084)	-1.61	0.11
Provisioning interval	Group	Intercept	0.318 (\pm 0.054)	5.90	<0.0001
		Group: MaleClip	-0.007 (\pm 0.094)	0.08	0.94
		Group: FemaleClip	0.026 (\pm 0.083)	0.31	0.76
Time on water	Trip duration + Sex	Intercept	2.032 (\pm 0.059)	34.59	<0.0001
		Trip duration	0.421 (\pm 0.014)	30.55	<0.0001
		Sex: Male	-0.235 (\pm 0.074)	-3.16	0.0016
Number of landing	Trip duration + Sex + Treatment	Intercept	4.709 (\pm 0.048)	98.23	<0.0001
		Trip duration	0.361 (\pm 0.012)	30.05	<0.0001
		Sex: Male	-0.211 (\pm 0.048)	-4.41	<0.0001
		Treatment: Clip	-0.074 (\pm 0.056)	-1.31	0.192
		Treatment: Partner	-0.123 (\pm 0.058)	-2.13	0.033
2013					
Trip duration	Treatment	Intercept	0.393 (\pm 0.051)	7.63	<0.0001
		Treatment: Clip	0.166 (\pm 0.070)	2.38	0.017
		Treatment: Partner	-0.021 (\pm 0.066)	-0.31	0.76
Provisioning interval	Treatment	Intercept	0.181 (\pm 0.046)	3.97	<0.0001
		Treatment: Clip	0.002 (\pm 0.056)	0.04	0.97
		Treatment: Partner	-0.097 (\pm 0.055)	-1.76	0.078
Time on water	Trip duration + Sex + Treatment + Trip duration \times Treatment	Intercept	1.612 (\pm 0.060)	26.74	<0.0001
		Trip duration	0.574 (\pm 0.034)	17.15	<0.0001
		Sex: Male	-0.055 (\pm 0.034)	-1.62	0.10
		Treatment: Clip	0.274 (\pm 0.078)	3.53	0.0004
		Treatment: Partner	-0.072 (\pm 0.077)	-0.94	0.35
		Trip duration \times Treatment: Clip	-0.122 (\pm 0.041)	-2.99	0.0028
Number of landing	Trip duration	Trip duration \times Treatment: Partner	0.022 (\pm 0.045)	0.49	0.63
		Intercept	4.801 (\pm 0.060)	80.3	<0.0001
		Trip duration	0.437 (\pm 0.019)	23.6	<0.0001

Table 3.7 Indices of the condition of chicks from clipped and control nests in 2012 and 2013. Pairs of values that differ significantly are indicated with matching superscripts. Fledging success and body mass at peak differed between years, with chicks heavier and successfully fledged in 2013 on average.

	2012			2013		
	Control	Male-clipped	Female-clipped	Control	Male-clipped	Female-clipped
Number of monitoring nests	17	11	11	11	12	10
Fledging success (individuals)	10	5	7	8	11	9
Age at peak (days)	59 ± 11 ^a	45 ± 5 ^a	57 ± 12	59 ± 4	61 ± 9	58 ± 6
Age at fledging (days)	82 ± 6 ^b	70 ± 6 ^b	79 ± 6	81 ± 5	81 ± 2	83 ± 3
Growth rate (g day ⁻¹)	14.49 ± 5.42	16.45 ± 5.43	12.97 ± 3.98	15.18 ± 2.98	15.46 ± 3.03	15.27 ± 3.84
Body mass at peak (g)	586 ± 71	539 ± 72	545 ± 79	645 ± 57	650 ± 83	650 ± 99
Body mass at fledging (g)	509 ± 95 ^c	330 ± 63 ^c	442 ± 108	548 ± 68	564 ± 58	549 ± 83

3.7. Appendices

Appendix 3.1 Equation for age estimation in shearwater chicks

Although offspring age is an important factor in many areas of ecology, it is difficult to directly observe hatching date without disturbance. I therefore developed an equation to estimate the age of shearwater chicks based on data collected on Awashima Island for 13 chicks in 2012. The hatching dates of the chicks were determined by daily direct observation using a small camera with an infrared source from 10-24 August. I assumed that the day of the first observation of a chick was the hatching date, and assigned the chick an age of one day. After hatching, the burrows were monitored every 4-8 days until fledgling, and three body size variables of the chicks were measured: (1) bill length (BL), i.e. the distance between the anterior edge of the nostrils and the bill tip; (2) wing length (WL), with the wing flattened and flexed at the wrist, measured from the tip of the wrist to the distal end of the phalanges or the end of the outer primary (once the outer primary had erupted); and (3) tarsus length (TL), with the leg flexed from the pit at the junction of the tibiotarsus and the tarsometatarsus to the distal end of the tibiotarsus. The BL and TL measurements were taken with a caliper to the nearest 0.05 mm, and WL was measured with a ruler to the nearest 1 mm.

I derived the relationships between age and the three body size variables using a nonlinear mixed model (using the maximum-likelihood method), with burrow ID as a random effect to account for the non-independence of subsequent measurements of the same chick. The equations for the two sigmoidal models used were as follows: the logistic model,

$$Y = \frac{A}{1+de^{-kX}}$$

and the Gompertz model,

$$Y = Ae^{-de^{-kX}}.$$

In these equations, Y represents body size (BL, WL and TL, respectively), A is the asymptote, k is the growth-rate constant, X is age, and d is a fitted constant. The Akaike information criterion (AIC) was used for model selection. To assess the range of error in estimating chick age using the predictive equations, I used a cross-validation approach, such that the birds used to develop the predictive equation were also used to validate it (Halsey et al. 2008). The model selected by AIC was run 13 additional times, each time with a different individual bird omitted from the analysis. After each iteration, the resulting model was used to predict the age of the omitted bird and then compared to the actual age of that bird. The accuracy and precision of the model was evaluated based on arithmetic error (i.e. estimated age – actual age) and 95% confidence intervals for every five-day age interval, respectively.

Thirteen of the hatched chicks fledged between 22 October and 15 November, and the mean age at fledging was 81 days (range: 65-89). Of the two sigmoidal models tested, the growth curves of BL and TL fitted the logistic model better than the Gompertz model, whereas the growth curve of WL fitted the Gompertz model better (Figure S3.1.1, Table S3.1.1). The equations for estimating chick age were obtained by transformation of the selected models as follows:

$$\begin{aligned}age &= -15.38 \ln \left[\left(\frac{50.50}{BL} - 1 \right) / 1.719 \right] \\age &= -41.67 \ln \left[-0.278 \ln \left(\frac{WL}{527.90} \right) \right] \\age &= -9.71 \ln \left[\left(\frac{52.63}{TL} - 1 \right) / 1.918 \right].\end{aligned}$$

The cross-validation analysis provided the accuracy (mean arithmetic error) and precision (95% confidence intervals) of the age estimations based on each of the body measurements (Figure S3.1.2, Table S3.1.2). All body measurements showed high

accuracy (error within 1.5 days) in the age range 16-40 days (Table S3.1.2). However, the accuracy of ages estimated based on BL and TL decreased from age 41 days, whereas the ages estimated based on WL maintained their accuracy within 1.5 days until age 80 days (Table S3.1.2). Overall, therefore, WL is the most appropriate measurement for estimating the age of streaked shearwater chicks.

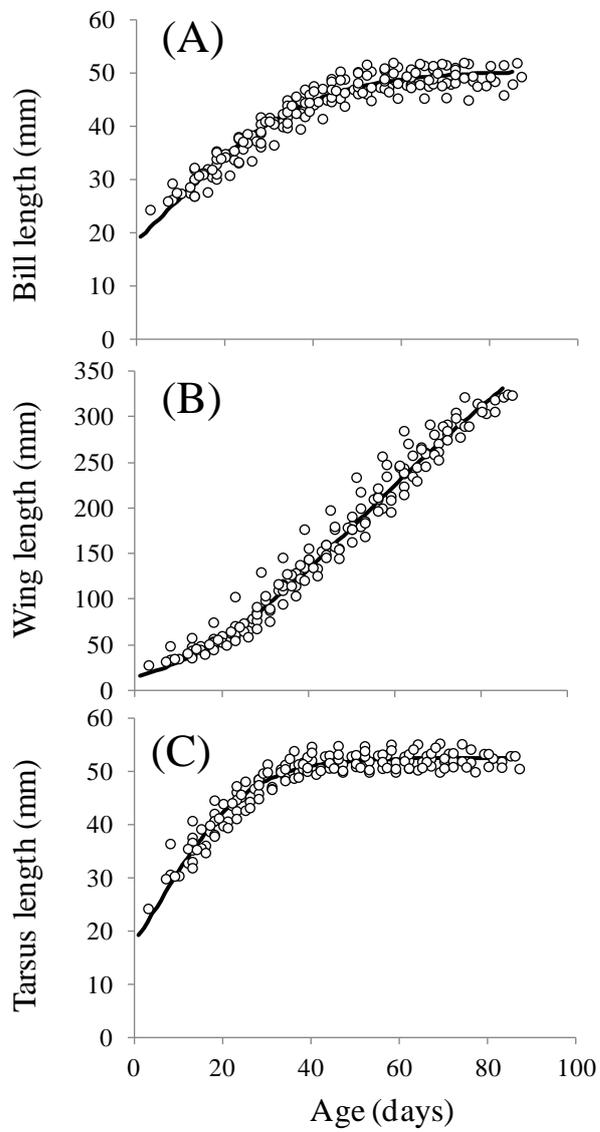


Figure S3.1.1.

Increase in the (A) bill, (B) wing, and (C) tarsus length of streaked shearwater chicks.

Solid lines indicate nonlinear mixed models selected using AIC (see also Table 3.1.1).

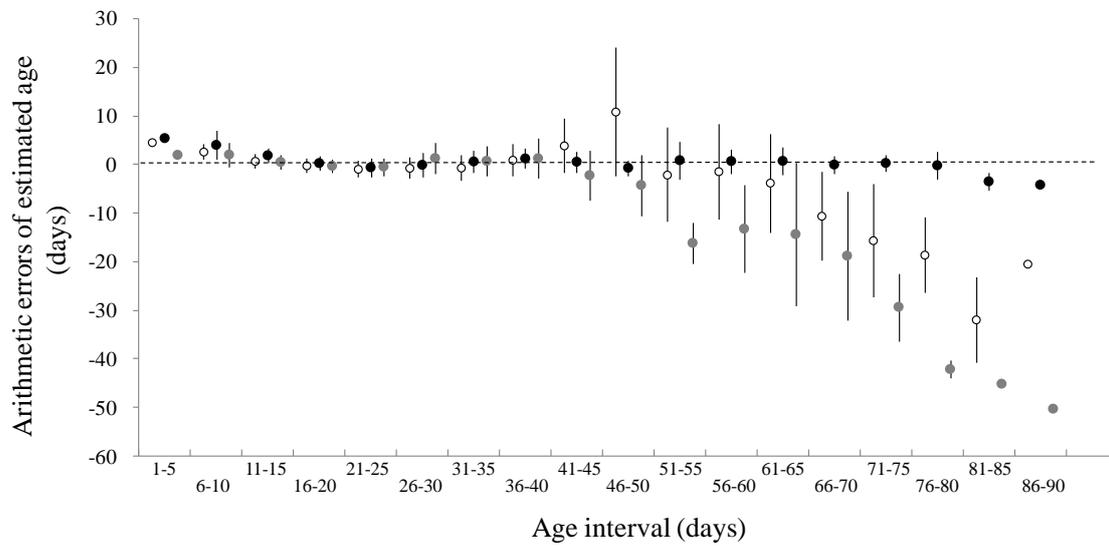


Figure S3.1.2.

Relationship between age classes of shearwater chicks and arithmetic error in chick age estimated based on bill (open), wing (closed), and tarsus lengths (grey circles). Vertical lines represent 95% confidence intervals (see also Table 3.1.2).

Table S3.1.1 Estimated parameters of two nonlinear mixed models relating body size (Y) to age of Streaked Shearwater chicks.

Model	AIC	Fitted constant (d)	Growth-rate constant (k)	Asymptote (A)
Bill length				
Logistic	451.7	1.719	0.065	50.50
Gompertz	503.6	1.136	0.052	51.13
Wing length				
Logistic	1070.5	15.627	0.054	376.21
Gompertz	1064.1	3.596	0.024	527.90
Tarsus length				
Logistic	360.6	1.918	0.103	52.63
Gompertz	421.7	1.328	0.089	52.80

Table S3.1.2 Arithmetic errors of estimated age by body sizes in relation to age intervals in Streaked Shearwater chicks

Age interval	Bill length			Wing length			Tarsus length		
	Mean arithmetic error (days)	95% confidence interval	n	Mean arithmetic error (days)	95% confidence interval	n	Mean arithmetic error (days)	95% confidence interval	n
1-5	4.6	-	1	5.5	-	1	2.0	-	1
6-10	2.7	1.6	5	4.1	2.9	5	2.1	2.5	5
11-15	0.8	1.4	11	1.9	1.4	11	0.6	1.4	11
16-20	-0.1	1.5	13	0.3	1.5	13	-0.2	1.4	13
21-25	-0.9	1.7	13	-0.5	2.0	13	-0.4	1.8	13
26-30	-0.6	2.2	12	0.0	2.4	12	1.4	3.3	12
31-35	-0.6	2.6	12	0.7	2.2	12	0.8	3.1	11
36-40	1.0	3.3	13	1.3	2.1	13	1.3	4.1	10
41-45	4.0	5.6	11	0.6	2.1	11	-2.2	5.2	8
46-50	10.9	13.3	11	-0.7	1.6	12	-4.2	6.3	8
51-55	-2.1	9.7	6	0.9	3.9	8	-16.1	4.3	3
56-60	-1.3	9.8	8	0.7	2.5	13	-13.2	8.9	7
61-65	-3.7	10.2	9	0.8	2.8	12	-14.3	14.7	7
66-70	-10.5	9.0	8	0.0	1.8	12	-18.7	13.2	6
71-75	-15.6	11.7	5	0.3	1.7	10	-29.3	7.0	4
76-80	-18.5	7.7	5	-0.1	2.9	5	-42.1	1.8	2
81-85	-31.9	8.8	3	-3.4	1.7	4	-45.1	-	1
86-90	-20.4	-	1	-4.1	0.2	2	-50.2	-	1

Appendix 3.2 Extraction of nest attendance from wet/dry data for shearwater parents

To understand seabird reproductive strategies, it is fundamentally important to know how often the birds return to their nest. Nest attendance by free-ranging seabirds has been investigated using a wide range of methods, ranging from visual observations, radio transmitters, and electric balances, to more advanced devices such as time-depth recorders (Trembley et al. 2003, Hamer et al. 2006, Ochi et al. 2010, Linnebjerg et al. 2014). Few of these methods, however, have the combined advantages of low disturbance levels, long-term deployment and a high degree of accuracy. Now, however, miniature leg-mounted data-loggers, which continuously record wet/dry states, are available in a size that can be attached to the legs of medium-sized seabirds. Since most shearwaters and petrels return to their nests at night to provide their chicks with food (Warham et al. 1990), a prolonged nocturnal dry period presumably suggests nest attendance. One advantage of the leg-mounted data-loggers is that long-term deployments are possible; hence it may be possible to infer nest attendance by nocturnal shearwaters throughout the chick-rearing period. Here I developed a method for estimating nest attendance based on data collected on Awashima Island using nine streaked shearwaters in 2012.

Actual nest attendance was determined using the radio frequency identification (RFID) system (Yamamoto et al. 2013). I fitted the RFID tags (22 mm in diameter \times 3 mm thick, weighing 1.5 g) and leg-mounted data-loggers (Mk3005: 16 mm \times 14 mm \times 6 mm, Biotrack Ltd., UK) to the birds' right and left tarsi, respectively, using plastic leg bands, at the end of August. The birds were immediately released back into their nest burrows. I then recaptured all birds between 17 September and 20 October and

downloaded all data successfully. The leg-mounted data-loggers recorded the timing of all changes of state (from wet to dry and vice versa) lasting 6 s or more. The RFID system I used comprised a reader, six antennae and water-proofed tags (Yamamoto et al. 2013). I also measured the chicks from the experimental nests on 1 September to estimate their age based on wing length (Appendix 3.1).

If the RFID antenna detected nest attendance by a bird at night, I extracted the continuous dry duration for the same period that the data-logger for that bird had recorded. If the RFID antenna did not detect nest attendance on a particular night, I extracted the longest continuous dry duration (i.e. longest continuous flight) for that night. There were only three bird-nights with continuous dry durations of more than four hours but without detection by the RFID system. However, since the streaked shearwaters in my study had maximum continuous flight durations of 2.44-3.78 h during the day, I assumed that the continuous dry durations of more than four hours at night represented a nest attendance detection failure by the RFID system, and eliminated those data from all subsequent analyses. I analyzed actual nest attendance (return/not return) by means of a generalized linear mixed model (GLMM) with the dry duration measured by the data-logger as the fixed effect and individual identity as a random effect, using a binomial error distribution. To investigate the effect of chick age, I divided the dataset into three groups according to chick age: A) ≤ 19 days; B) 20–39 days; and C) ≥ 40 days.

The models for the two younger chick age classes (A and B) had a discriminatory power of 93% (56/60) and 96% (73/76), respectively, while the model for the oldest chick age class (C) only correctly classified 75% (48/64) of nest attendance events (Figure S3.2.1, Table S3.2.1). The decrease in discriminatory power may be the result of a decrease in continuous dry duration at night during the late

chick-rearing period (Figure S3.2.2). This result indicates that wet/dry data make it possible to infer nest attendance by streaked shearwaters during the early and middle chick-rearing periods.

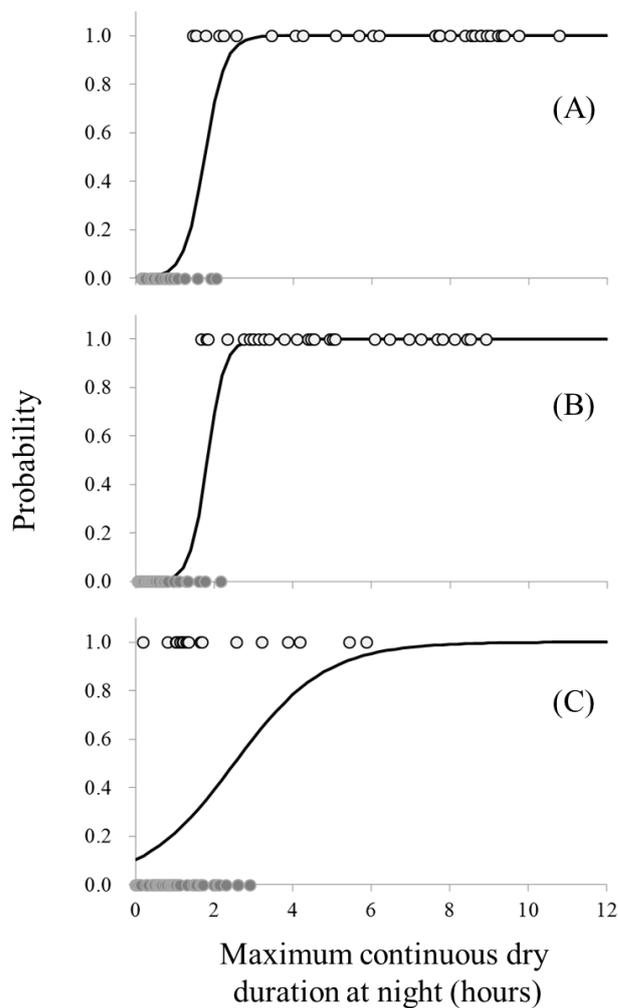


Figure S3.2.1.

Relationship between maximum continuous dry duration at night, recorded by an animal-borne data-logger, and the predicted probability of return to the burrow during the night in streaked shearwaters with a chick (A) ≤ 19 days old, (B) 20–39 days old, and (C) ≥ 40 days old. Open and filled symbols represent birds that returned and did not return to the nest, respectively. Predicted probabilities are based on a generalized linear mixed model with a binomial error structure.

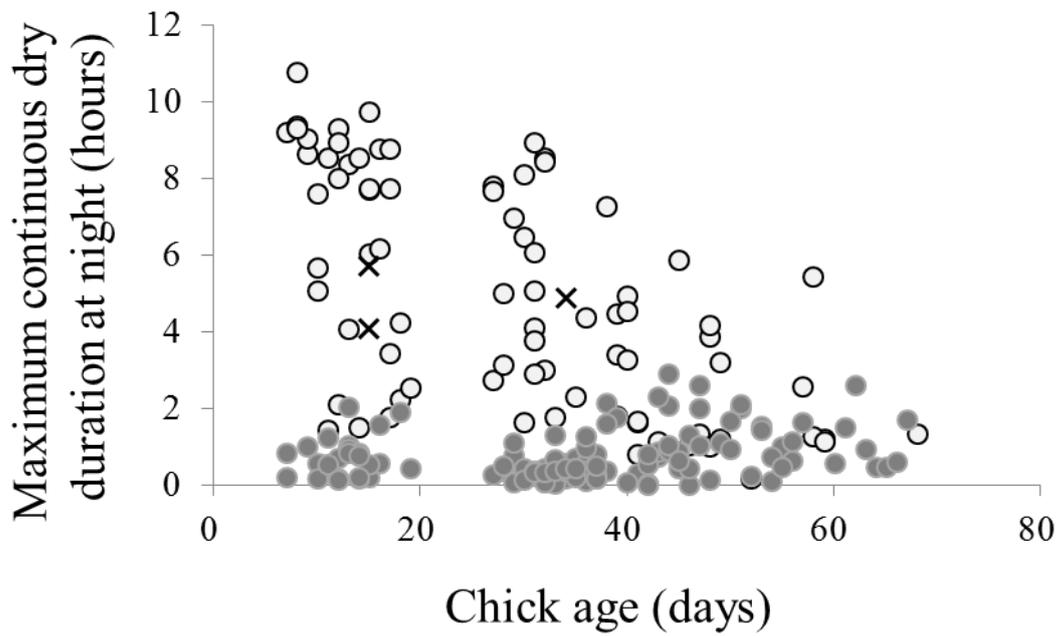


Figure S3.2.2.

Relationship between chick age and maximum continuous dry duration at night experienced by the parents. Open and filled symbols represent birds that returned and did not return to the nest, respectively, measured using the radio frequency identification (RFID) system. Crosses represent data that were eliminated from all analyses, because of an assumed failure to detect nest attendance by the RFID system (see text for further details).

Table S3.2.1 Verification by generalized linear mixed models for accuracy of predicted attendance against actual nest attendance measured using radio frequency identification system in streaked shearwater

Model	Chick age interval	Total number of attendance	Threshold (min)	Actual nest attendance	Predicted nest attendance	
					existence	non-existence
1	1-19	60	104	existence	30	2
				non-existence	2	26
2	20-39	76	109	existence	26	2
				non-existence	1	47
3	40 <	64	151	existence	6	13
				non-existence	3	42

Chapter 4:

General Discussion

4.1. Precision and accuracy of the doubly labeled water method

The precision and accuracy of metabolic rates measured using the doubly labeled water (DLW) method with high levels of isotope elimination was systematically investigated by comparison with metabolic rates measured using respirometry (Chapter 2). My results suggest that precision of the DLW method increases in response to increases in the extent of isotope elimination (longer experimental periods or higher metabolic rates). I also confirmed that the DLW method provides robust metabolic estimates in the field, which are correlated with foraging activities (Chapter 3). These results may settle the differences between conclusions regarding the DLW method resulting from validation in the laboratory (low precision: Butler et al. 2004) and empirical studies in the field (sufficient precision: Peterson et al. 1998, Shaffer 2011).

On the other hand, this study revealed an important problem. High isotope elimination while using the DLW method decreased the accuracy of estimated metabolic rates. This reduced accuracy may be the result of a mismatch between the assumptions of the DLW method and the physiological conditions of a subject species. A basic assumption of the DLW method for measuring metabolic rate is that the hydrogen isotope (^2H) in body water only leaves the body as water (Speakman 1997). Similarly, the oxygen isotope (^{18}O) is expected to only leave the body as water and CO_2 . Thus, any loss of isotopes in other products will introduce inaccuracy into this method. For instance, a previous validation study found an overestimation of the CO_2 production rate for California sea lions, and suggested that part of this discrepancy was the result of incorporation of ^{18}O into urea (Boyd et al. 1995). Similarly, loss of ^2H via fatty acid synthesis would result in an underestimate of CO_2 production rate (Haggarty et al. 1991). For seabirds, there is extremely limited information on the loss of isotopes in body products, which may influence the accuracy of the DLW method. This method

should therefore be used with caution, especially when characterizing inter-species differences in field metabolic rates for seabirds. Further exploration of the cause of inaccuracies in the DLW method should reveal the elimination routes of injected isotopes, using subjects with a variety of physiological backgrounds (e.g. divers vs. flyers, polar species vs. tropical species).

4.2. Energetic response to poor energy availability

In my study, streaked shearwaters reduced their field metabolic rate (FMR) in response to poor energy availability in 2012. Some seabirds also reduce their rate of energy expenditure when the environmental energy supply is limited (kittiwakes in the Pacific Ocean: Jodice et al. 2006; little auks: Welcker et al. 2009b), but others do not (thick-billed murre: Kitaysky et al. 2000, kittiwakes in the Atlantic Ocean: Welcker et al. 2010). Although opposite results have been found for different populations of kittiwakes, there are consistent differences in life history traits between these two populations: Pacific kittiwakes live longer but have lower fecundity than Atlantic kittiwakes (e.g. Coulson 2002, Schultner et al. 2013). Long-lived mammals such as monkeys and humans also decrease their metabolic rates in response to energy restriction (Heilbronn et al. 2006, Anderson et al. 2009, Redman et al. 2009, Yamada et al. 2013). For instance, studies of humans have found significant decreases in the resting and field metabolic rates of individuals subjected to energy restrictions lasting several months (Heilbronn et al. 2006, Redman et al. 2009). These findings imply that animals with longer life-spans have the capacity to adjust their FMR to compensate for poor food availability.

It is widely accepted that energy restrictions delay the onset of aging and extend the lifespan of diverse animal species, including worms, flies, rodents and

monkeys (Masoro 2002). In nonhuman primates, energy restriction has been shown to reduce or delay the onset of diverse age-related disorders, such as diabetes (Gresl et al. 2001) and immune senescence (Messaoudi et al. 2006). On the other hand, in poultry species, short-term food restrictions have been shown to reduce egg production and affect reproductive endocrinology (Holmes et al. 2003, Ottinger et al. 2005). These findings imply that limited energy availability may result in both longer lifespans and lower fecundity, which corresponds to the life history traits of long-lived animals, although the physiological effect of energy restriction on avian species remains unexplored (Holmes and Martine 2009). Further research into the physiological mechanisms, such as hormones and the immune system, associated with reduced FMRs in poorer energy availability conditions, may contribute to our understanding of the evolutionary processes behind the life history strategies of animals faced with environmental fluctuations.

4.3 Decisions about energy allocation between current reproduction and survival

My results demonstrated that chick-rearing streaked shearwaters possess both flexible and fixed investment strategies (Chapter 3; Figure 4.1, Table 4.1). Depending on energetic requirements, the birds made use of several options for time and energy allocation when using their flexible foraging strategy (Figure 4.2). Under poor breeding conditions, they prioritized maintaining their body mass over their chick's condition. This result is consistent with the prediction of life history theory that long-lived seabirds should prioritize self-maintenance over their current reproductive attempt (Stearns 1992). This finding also supports the theoretical model developed by Erikstad et al. (1998), which predicts that when food is abundant, parents can easily compensate for increased costs, whereas food shortages may render them unable to do so.

Even within Procellariiformes, the conclusions of previous studies involving experimental increases in flying cost have been equivocal: parents in some studies passed the additional costs on to their chicks and/or partners, while those in others managed to compensate for the increased costs on their own (Table 4.2). However, since most of these studies were conducted in a single year, the impact of energy availability has largely been ignored. Thus, studies in which subjects responded flexibly to manipulation may have overlooked the effect of energy availability and the flexible foraging strategies of the subject species. In addition, even though the body mass of handicapped parents decreased, the handicapped individuals may have adaptively reduced it to compensate for the higher flight costs imposed by feather clipping or extra weight (Norberg 1981, Pennycuik 1989), independent of decisions regarding investment strategies. In one case, the body mass of breeding feather-clipped thin-billed prions *Pachyptila belcheri* declined through the experiment, while that of non-clipped single birds that had been separated from their mates, remained stable (Weimerskirch et al. 1995). Conversely, chicks fledged by the single birds were lighter than those of control birds, while the clipped birds maintained the body mass of their chicks at the same level as control birds. The clipped birds therefore appeared to invest in the current reproductive attempt rather than future reproduction, which contradicts the finding for the single birds, which experienced a larger negative energetic balance but maintained their body mass. Thus, clipped individuals may, in some cases, be able to optimize their flight performance rather than investment allocations. This suggests that to develop a full understanding of the ultimate decisions birds make regarding their investment strategies for reproduction, it is important that experimental designs eliminate other factors that may influence body conditions in parents and chicks.

In my results, when streaked shearwaters faced the limits of their flexible foraging strategy, they prioritized their own survival and transferred the additional costs to their chicks, as predicted by life history theory (e.g. Stearns 1992). A seminal paper (Pianka 1976) recommended attempting to merge aspects of optimal foraging theory with the theory of optimal reproductive strategies, to specify some of the rules by which foraging input (i.e. energy) is translated into reproductive output (i.e. fitness). However, including this study, only four seabird species (streaked shearwater, little auk, thick-billed murre and black-legged kittiwake) have been investigated with respect to both foraging and reproductive efforts under different energy availability (Table 4.3). Of the other three species studied using feather clipping, only thick-billed murres showed a fixed investment strategy, even under favorable conditions (Jacobs et al. 2013). Since chick-rearing by thick-billed murres is expected to operate close to their intrinsic metabolic ceiling, independent of extrinsic factors (Kitaysky et al. 2000), a slight increase in FMR may directly influence reproductive decisions in the absence of flexible options for foraging. Both clipped black-legged kittiwakes and little auks showed flexible investment strategies, but the studies were conducted under relatively favorable breeding conditions for each species (Harding et al. 2009, Leclaire et al. 2011). In addition, both of those species adopt flexible foraging strategies in response to local conditions (Suryan et al. 2000, Welcker et al. 2012). Thus, the results of Harding et al. (2009) and Leclaire et al. (2011) may only reflect the birds' flexibility with respect to foraging decisions in response to additional costs when food is abundant. Further studies on the life history strategies of other seabirds using the approaches adopted in this study, which combined observations of behavioral and physiological flexibility, will provide a better understanding of the species-specific investment decision patterns of

parental seabirds, and also highlight the broad patterns of their adaptation to stochastic marine environments.

4.4 Figures and Tables

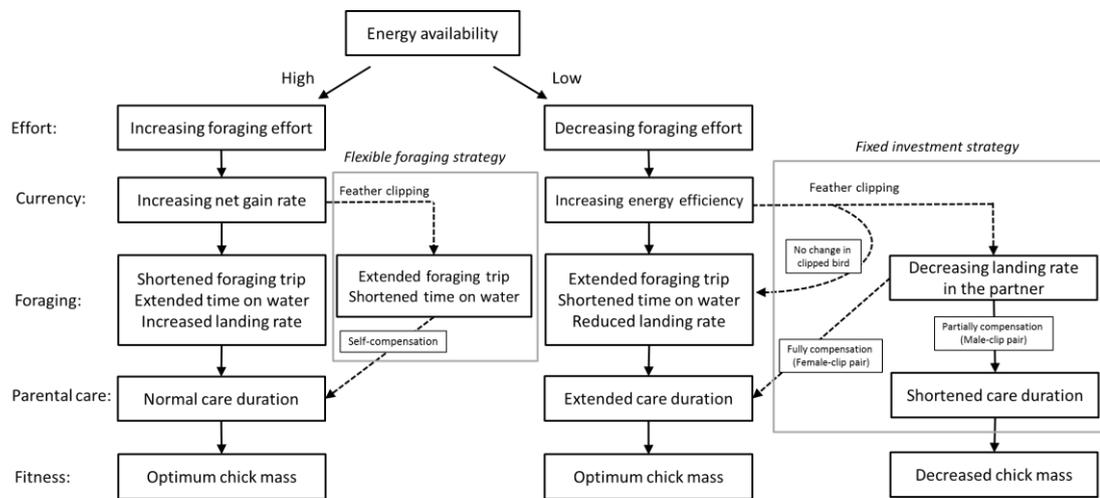


Figure 4.1.

A scenario for the impact of different levels of breeding conditions on foraging behavior and reproductive performance by parents.

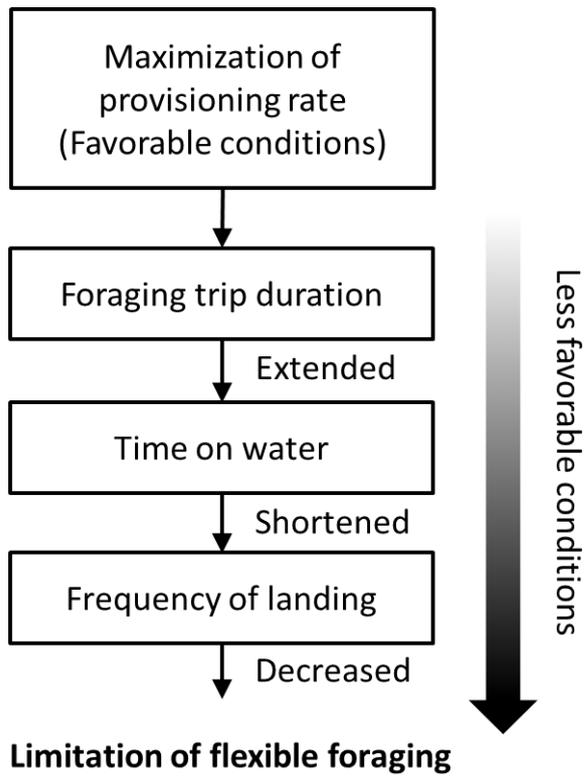


Figure 4.2.

A series of potential alterations in foraging behavior associated with changes in breeding conditions.

Table 4.1 A summary of the results of the foraging and reproductive experiments in Chapter 3

Experiment	Trait	2012	2013	Sex-related
Foraging experiment	Trip duration	Long	Short	
	% Total body water	Low	High	
	Field metabolic rate	Low	High	
	Energy intake rate	Equivalent	Equivalent	
Reproductive experiment	Sea surface temperature	High	Low	
	Control individuals			
	- Trip duration	Long	Short	
	- Provisioning interval	Long	Short	
	- Frequency of landings	Low	High	Female > Male
	- % Time on water	Low	High	Female > Male
	Response to feather clippings*			
	- Trip duration	Unchanged	Increased	
	- Provisioning interval	Unchanged	Unchanged	
	- Frequency of landings	Unchanged	Unchanged	2012: Female > Male
	- % Time on water	Unchanged	Decreased	2012: Female > Male
	Response of the clipped partner*			
	- Trip duration	Unchanged	Unchanged	
	- Provisioning interval	Unchanged	Unchanged	
	- Frequency of landings	Decreased	Unchanged	2012: Female > Male
	- % Time on water	Unchanged	Unchanged	2012: Female > Male
	Chick status			
	- Fledging success	Low	High	
	- Growth rate	Equivalent	Equivalent	
	- Peak body mass	Low	High	
- Age at peak*	Decreased**	Unchanged		
- Fledging body mass*	Decreased**	Unchanged		
- Age at fledging*	Decreased**	Unchanged		

* Analysis was conducted within each year to compare between the control and manipulated pairs.

** The drops were only observed in the male-clipped pair.

Table 4.2 Overview of handicapping studies that involved manipulation of flight performance in Procellariiformes

Species	Scientific name	Manipulation of foraging cost	Handicapped parent mass or condition	Chick mass or condition	Investment strategy	Reference
Streaked shearwater (favorable condition)	<i>Calonectris leucomelas</i>	Feather clipping	No change	No change	Flexible	This study
Streaked shearwater (unfavorable condition)	<i>Calonectris leucomelas</i>	Feather clipping	No change	Decrease	Fixed	This study
Yellow-nosed albatross	<i>Diomedea chlororhynchos</i>	Extra weight	Decrease	Decrease	Flexible	Weimerskirch et al. (2000c)
Antarctic petrel	<i>Thalassoica antarctica</i>	Extra weight	No change	-	Fixed	Saether et al. (1993)
Antarctic petrel (females)	<i>Thalassoica antarctica</i>	Extra weight	Decrease	-	Flexible	Tveraa et al. (1997)
Cory's shearwater	<i>Calonectris diomedea</i>	Feather clipping	No change	Decrease	Fixed	Navarro and González-Solís (2007)
Leach's storm-petrel	<i>Oceanodroma leucorhoa</i>	Feather clipping	No change	Decrease	Fixed	Mauck and Grubb (1995)
Thin-billed prion	<i>Pachyptila belcheri</i>	Extra weight	No change	No change	Flexible	Duriez et al. (2000)
Thin-billed prion	<i>Pachyptila belcheri</i>	Feather clipping	Decrease	No change	Flexible	Weimerskirch et al. (1995)
Antarctic prion	<i>Pachyptila desolata</i>	Extra weight	No change	-	Fixed	Weimerskirch et al. (1999)

Table 4.3 Overview of foraging and handicapping studies that involved manipulation of the flight ability of long-lived seabirds

Species	Scientific name	Field metabolic rate in poorer environment (Increase/Decrease/No change)	Handicapping studies that manipulated flight ability			Fledgling mass	Investment strategy	Reference
			Experimental duration (years)	Environmental condition	Handicapped parent mass			
Streaked shearwater	<i>Calonectris leucomelas</i>	Decrease	2	Unfavorable and favorable	No change	Decrease	Fixed	This study
Little auk	<i>Alle alle</i>	Decrease	2	Favorable (both)	Decrease	Decrease	Flexible	Harding et al. (2009), Welcker et al. (2009b)
Thick-billed murre	<i>Uria lomvia</i>	No change	1	Favorable	No change	Decrease	Fixed	Kitaysky et al. (2000), Jacobs et al. (2013)
Black-legged kittiwake*	<i>Rissa tridactyla</i>	Decrease	2	Favorable (both)	Decrease	No change	Flexible	Jodice et al. (2006), Leclaire et al. (2011)

*Black-legged kittiwake in North Pacific population

Acknowledgements

I am grateful to Mr. Tateo Honbo and Ms. Tsuguyo Honbo for their support in the field. I also thank many colleagues for their assistance in the field: Dr. Takashi Yamamoto, Ms. Madoka Yamaguchi, Ms. Akemi Ushijima, Mr. Yuki Tamura, Mr. Tomoya Abe, Ms. Emiko Oda, Ms. Kana Fujii, Mr. Masahiro Ogawa, Ms. Sakiko Matsumoto, Mr. Tatsuya Shiozaki, Mr. Masato Ohsugi, Mr. Kenta Kuzuya, Ms. Mariko Suhara, Ms. Miho Sakao, and Mr. Takanori Sugawara. I also wish to specially thank Dr. Carlos Zavalaga, Dr. Alice Carravieri and Dr. Martina Müller for their valuable suggestions on my research.

I would like to thank Dr. Naoki Tomita, Dr. Kentaro Kazama and the staff at the Meijo University for help with the isotope analysis. I also wish to thank Dr. Naoyuki Ebine, Dr. Yosuke Yamada, Mr. Takashi Oono, and Dr. John Speakman for technical advice on the doubly labeled water method. I have greatly benefited from Mr. Hiroki Kurazono, Dr. Hiroshi Yamamoto and Dr. Katsuyuki Yamazaki for developing and operating the radio frequency identification system.

I am deeply grateful to Dr. Satoko Kimura, Dr. Yuichi Mizutani, Mr. Fujii Hidenori, Dr. Yoshihiro Akiyama, Mr. Noelikanto Ramamonjisoa, Dr. Hiromi Yamashita, Ms. Yuko Shinohara and the members of Environmental Science Research Laboratory, Central Research Institute of Electric Power Industry, especially Dr. Rikyu Matsuki, Dr. Toru Takeuchi and Dr. Seiya Abe, for their encouragement to my work.

I greatly thank Dr. Kenichiro Sugitani and Dr. Yoshihiro Natsuhara for reviewing this thesis and providing comments to improve the manuscript. I am also deeply grateful to Dr. Nariko Oka, Dr. Maki Yamamoto and Dr. Yasuaki Niizuma for their considerable encouragement and invaluable discussion. Finally, I would like to

express my sincere gratitude to my supervisor, Dr. Ken Yoda for providing me this precious opportunity in his laboratory and allowing me to work at my own pace.

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