主論文

Flexible foraging behavior and associated physiological costs in chick-rearing streaked shearwaters

育雛期のオオミズナギドリの柔軟な採餌行動とそれに伴う生理的負荷

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Chapter 1. General introduction

1.1 Foraging behavior of long-lived animals influenced by external factors, internal factors, and reproductive trade-off

Long-lived wild animals face a challenge of balancing their own physiological condition and reproductive performance by modifying their foraging behavior in response to their surrounding environment. Wild animals must determine their foraging site or duration based on external factors in their habitat, such as the geographical distribution of their food (Kitaysky et al., 2010; Henderson et al., 2017). Their physiological condition could influence (Angelier et al., 2008; Crossin et al., 2012) and be influenced by their foraging behavior (Zera & Harshman, 2001; Henderson et al., 2017). Moreover, long-lived animals face a trade-off between current and future reproduction to maximize their fitness, where foraging is influenced by current offspring demand or prospect of future reproduction (Erikstad et al., 1998; Rivalan et al., 2005; Hamel & Côté, 2008; Scharf et al., 2013). Thus, wild animals could have evolved to adapt to shifting habitats on an annual basis while maintain their physiological condition and current reproductive performance to some extent (Weimerskirch et al., 1995).

1.2 Long-lived seabirds breeding in the dynamically changing marine ecosystem

The marine top predators must adapt to forage in high food availability areas that are patchy and unstable. This is due to the dynamic fluctuations of the feeding habitat in the complex physical environment of the ocean. In the pelagic marine ecosystem, a mixing of cold water and warm current creates upwelling which is a phenomenon of rising seawater from the deeper regions to the surface (Demarcq et al., 2003). By upwelling, nutrient-rich sea water is brought up to the surface where phytoplankton use it for photosynthesis (Qiu, 2019). The high abundance of phytoplankton increases the amount of zooplankton, which is food for small fish, resulting in high food availability for marine top predators (Thayer & Sydeman, 2007; Thompson et al., 2012; Anguita & Simeone, 2015).

Seabirds, one of the top predators in the marine ecosystem, are highly mobile and are widely distributed in the marine environment. They have a long-lived and have reproductive characteristics such as delayed reproduction, slow offspring growth, and high survival rate (Hamer et al., 2001). They usually breed in colonies and on the same island every year. During the chick-rearing period, they take round excursions from the breeding colonies to the feeding sites (hereafter referred to as foraging trips) to sustain both, their offspring and themselves. To feed their chick regularly, the seabirds must forage within the limitation of foraging habitat range and duration (Berrow et al., 2000; Shaffer et al., 2003; Robertson et al., 2014).

1.3 Seabirds' foraging behavior and reproductive trade-off

Foraging behavior of seabirds, their physiological condition, and their reproductive performance could be directly and indirectly influenced by their food availability in the surrounding environment (Figure 1.1). First, foraging behavior of seabirds is influenced by their food availability, which is indicated by the presence of other marine predators and physical oceanographic features. On a local scale, seabirds have been observed to congregate and forage in high marine productivity areas, with other predators such as other seabirds, large fish, and dolphins from the sea boundary layer (Evans, 1982; Silverman et al., 2004; Hebshi et al., 2008; Thiebot & Weimerskirch, 2013; Thiebault et al., 2014; Tremblay et al., 2014). Seabirds often use other predators as landmarks of high food availability areas for efficient foraging (Veit & Harrison, 2017; Bastos et al., 2020; Garrod et al., 2021) and thus, the intra- and interspecific relationship could influence foraging behavior and distribution of seabirds. The marine physical environment is also related to foraging behavior of the seabirds, as revealed by combining the bio-logging technique, a contemporary focal approach for recording wild animal movements (Yoda, 2019), and the satellite marine monitoring method (Pinaud & Weimerskirch, 2005; Grémillet & Boulinier, 2009; Kappes et al., 2010; Kowalczyk et al., 2015). Sea surface temperature (SST), in particular, influences the seabird foraging behavior, such as their distribution, foraging duration, and distance from the colony (Weimerskirch et al., 2001; Pinaud et al., 2005; Paiva et al., 2013; Serratosa et al., 2020); hence, SST is frequently used as an indicator of food availability of seabirds. The food availability in the surrounding could directly influence the parental physiological condition (Harding et al., 2013; Beaulieu et al., 2015; Laranjeiro et al., 2020) and reproductive performance of seabirds (Jenouvrier et al., 2018). Second, the physiological condition of seabirds' parents is determined by the foraging behavior associated with the surrounding environment. Active movement, such as foraging behavior, can cause physiological costs, which can be offset by resting or receiving nutrients (Zera & Harshman, 2001). Moreover, the physiological condition could determine foraging behavior, such as individuals with high physiological costs increase foraging effort (Angelier et al., 2008; Kroeger et al., 2019). Finally, parental behavior is related to their reproductive outcomes, such as chick development. Parental foraging behavior and obtaining plenty of food could increase the rate of the chick development (Weimerskirch et al., 2001), and the foraging behavior could be affected by food demands from chicks (Ochi et al., 2010; Ogawa et al., 2015). Ultimately, based on the food availability, parents of seabirds reduce their investment in current reproduction or can buffer the influence on their chick (Quillfeldt et al., 2007; Kidawa et al., 2017; Schoen et al., 2018).

As a result, a causal relationship must be observed between the surrouding environment, seabird foraging behavior, physiology condition, and reproductive performance. However, the complex links and direction of causality between marine environments, seabird foraging behavior, their physiological condition, and reductive performance are largely unexplored. That is particularly because no valid index has been established to quantify the physiological fatigue and capacity of recovery capacity associated with the foraging behavior of seabirds, prey resources are patchily distributed and often ephemeral, making them difficult to measure, and to accumulate long-term (decadal scale) and amount data set of seabirds' foraging behavior.

1.4 Aims of this thesis

The final goal of this thesis is to discuss the causal relationship between the surrounding environment, seabird foraging behavior, physiological condition, and reproductive performance. Following objectives are set to achieve this aim: 1) quantify the physiological fatigue and capacity of recovery, oxidative stress, associated with seabird foraging behavior; 2) determine the effects of other marine top predators on seabird foraging behavior; 3) reveal the causal relationship between the physical marine environment, foraging behavior, and reproductive performance.

Here, I have focused on chick-rearing streaked shearwaters (*Calonectris leucomelas*) (Figure 2.1) breeding on Awashima island, located in the Sea of Japan (detailed in chapter 2.1). In chapter 3, I examined the foraging behavior and associated oxidative stress, using data from chick-rearing streaked shearwaters in 2018 and 2019. In chapter 4, I have investigated the local and large-scale interspecific relationship between streaked shearwaters and larger fish, potentially sharing prey species with streaked shearwaters. In chapter 5, I have examined the relationship between foraging behavior of streaked shearwaters, their reproductive performance, and SST, to determine how streaked shearwaters buffer environmental change.

1.5 Figure

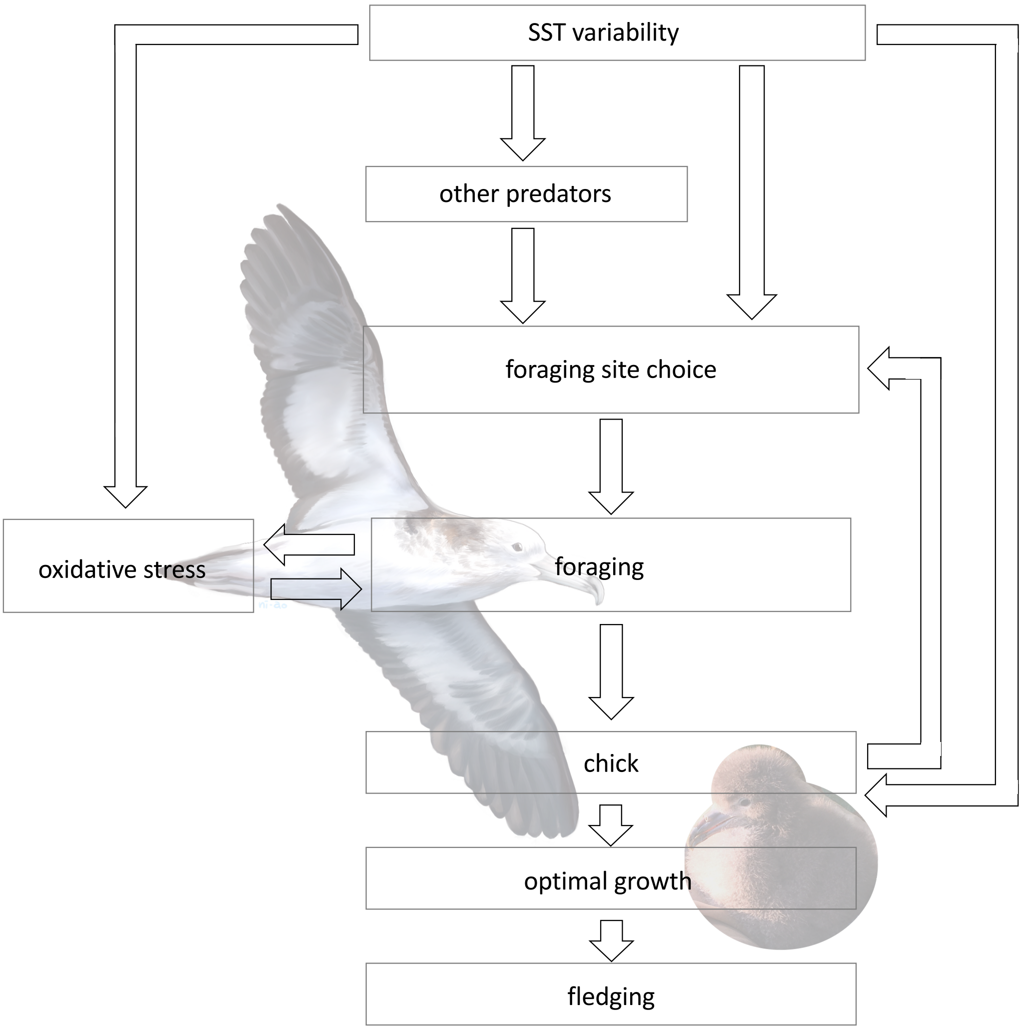


Figure 1.1: Conceptual diagram of the environment, behavior, physiological condition, and current reproductive performance. The arrows represent potential causal relationships.

Chapter 2. General method

2.1 Studied species and site

Seabirds, in the order Procellariiformes (shearwaters, albatrosses, and petrels), exhibit extreme life-history traits with low reproductive output such as, single egg laying, slow chick development, and high survival (Hamer et al., 2001; Weimerskirch, 2007). In an unsustainable environment, they perform foraging trips of varied durations (from one day to more than 10 days) to balance chick demand and their own physiological condition (Chaurand & Weimerskirch, 1994; Weimerskirch, 1998; Schultz & Klomp, 2000; Congdon et al., 2005; Ochi et al., 2016; Tyson et al., 2017).

Streaked shearwaters (Figure 2.1a, b), medium-sized seabirds in the Procellariiformes order, are distributed from 24-42°N and 121-142°E in East and Southeast Asia (Oka, 2004). In mid-March, streaked shearwaters migrate from wintering locations such as, northern New Guinea, the Arafura Sea, and the South China Sea to their breeding colony (Yamamoto et al., 2010). They lay a single egg in mid to late-June and the chick hatches sometime between early to mid-August. Afterwards, the chicks would be nourished by their parents until mid-October, when the parents migrate south, at which point they attain 130% of adult body mass, go through starvation for a few weeks, lose their body mass (Figure S5.2), and fledge in early November (Oka et al., 2002; Yoda et al., 2017; Figure 2.1c). Some Procellariiformes, including streaked shearwaters, can fly long distances almost without flapping wings, utilizing wind from the sea surface to save energy (Nourani & Yamaguchi, 2017; Mir et al., 2018). During the chick-rearing period (August to October), parents of streaked shearwaters make foraging trips to forage at the pelagic ocean and return to their nest at the night to feed their chick. To forage small pelagic fish, streaked shearwaters generally dive shallower than 3 m for fewer than 6 seconds (Matsumoto et al., 2012).

The studied colony of streaked shearwaters in Awashima, located in the middle east of the Sea of Japan (SOJ; 38°28′ N, 139°14′ E). SOJ is a semi-closed sea that connects the Japanese archipelago to the Eurasian continents (Figure 2.2a). During the chick-rearing period, streaked shearwaters make foraging trips every one d to 17 days (Figure 2.2b). In the SOJ, where Tsushima Warm Current transports warm and nutrient-poor water, flows to the northwest Pacific Ocean (PO) via the Tsugaru Strait (Figure 2.2a), and directly influences ecosystem dynamics in the SOJ (Onitsuka et al., 2007). Streaked shearwaters breeding on Awashima forage on small pelagic fish such as Japanese anchovy (*Engraulis japonicus*) and bullet mackerel (*Auxis rochei*; Kurasawa et al., 2012; personal communication, Yamamoto) with foraging trip from one to 12 days in the SOJ (average 1.5 days). Streaked shearwaters often fly through the Tsugaru Strait to the northwest PO, which is known to be one of the most productive fishing areas in the world due to the mixing of Oyashio Cold Current and Kuroshio Warm Current (Qiu, 2019; Figure 2.2a) with foraging trips lasting between two to 17 days (average 6.6 days). Streaked shearwaters have been reported to forage high-energy prey such as pacific saury (*Cololabis saira*) in the PO (Kurasawa et al., 2012; Ochi et al., 2016).

2.2 Field work and logger deployment

I conducted fieldwork on chick-rearing streaked shearwaters breeding on Awashima Island from August to November, corresponding from their chick-rearing to the fledging period. Chick-rearing streaked shearwaters were captured by hand when returning to their nest burrows at night to feed their chicks. All captured birds were placed in opaque cloth bags, which are less physiologically stressful than handling them directly (Müller et al., 2017). Animal-borne loggers were attached to back feathers of birds with waterproof tape (Tesa®; Beiersdorf AG, Hamburg, Germany) and cyanoacrylate glue (Henkel Loctite Adhesives Ltd., Hatfield, UK).

2.3. Analyses of GPS data

I removed low accuracy data, points with horizontal dilution of precision >7 (the higher the number, the lower the accuracy), from the GPS data. A foraging trip was defined as an extended trip of more than 3 km from the colony and more than 6 h because streaked shearwaters begin their foraging trips before sunrise and return within a 3 km radius of the breeding site a few hours before or after sunset (Shiomi et al., 2012), which is associated with more than 6 h at-sea time. The missing values were interpolated every 60 s excluding In cases when the missing intervals were greater than 10 min. I used the function “pprox.x.irts” in the “tseries” package (Trapletti et al., 2020) for the interpolation. Foraging trips completed by the end of September were used in this analysis because the number of returns to the colony decreased gradually thereafter. Foraging trips with missing information for more than 24 h or 40% of the total trip duration were removed from subsequent analyses. All analyses were performed using R version 4.0.3 (R Development Core Team, 2020).

2.4 Ethical note

This study was approved by the Animal Experimental Committee of Nagoya University (GSES2011–2021) and the Ministry of the Environment Government of Japan. GPS loggers attached to streaked shearwaters weighed less than 25 g, accounting for less than 5% of their mean body mass. Previous studies showed that the deployment of same-sized loggers have no adverse effects on behavior such as trip duration, feathers, and chicks of this species (Shiomi et al., 2012; Yoda et al., 2014). The experiments are unlikely to have adverse effects on the subsequent survival of the birds, as 84 individuals were succeeded to recapture in multiple years from 2011 to 2021.

2.5 Figures

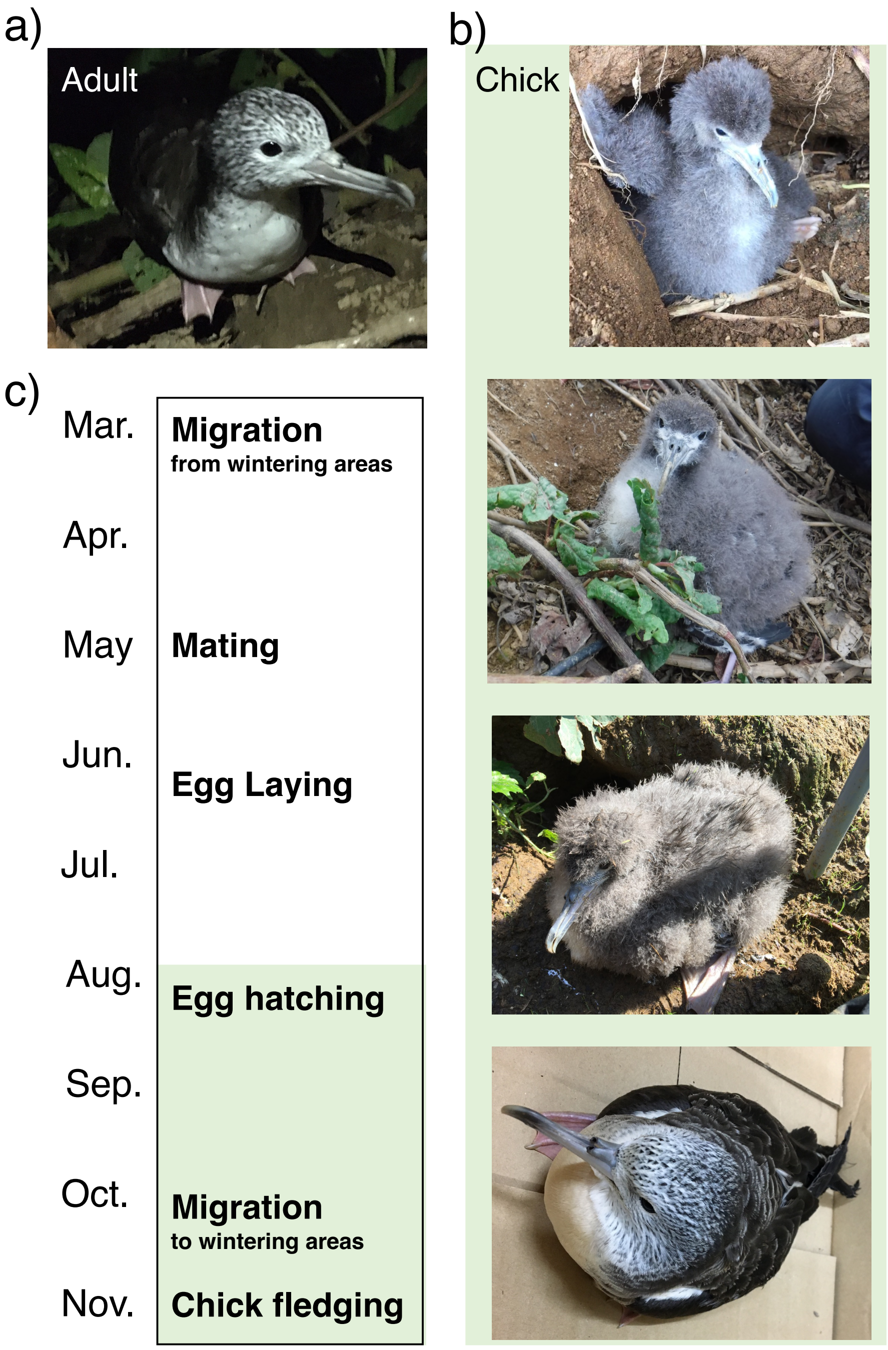


Figure 2.1: a) Image of an adult streaked shearwater. b) Images of streaked shearwater chicks at different growth stage (age representation: the chicks get older in images from top to bottom). c) Reproductive cycle of streaked shearwaters. The green area represents the field work period, which corresponding to the time period between hatching and chicks fledgling.

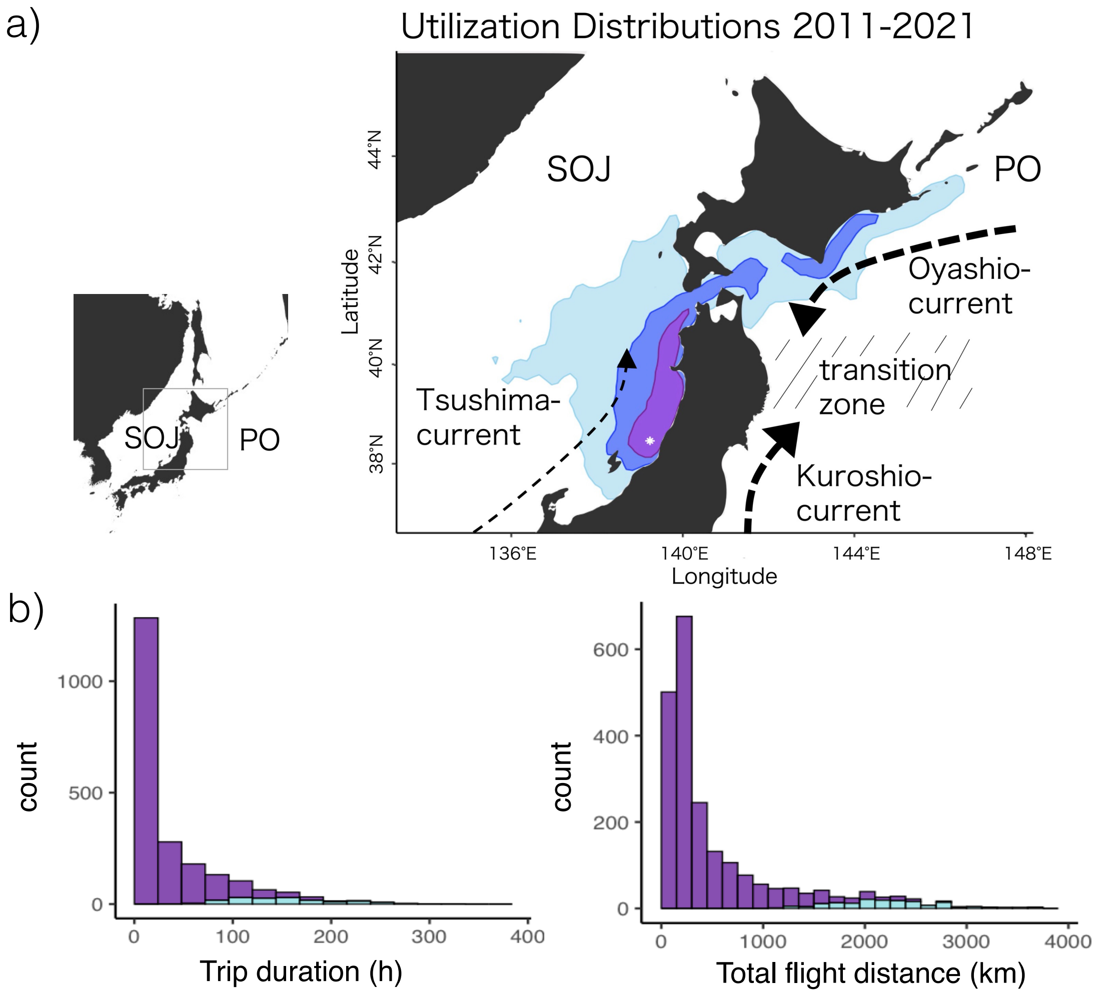


Figure 2.2: a) Utilization distributions (UD) of streaked shearwaters. The map on the left shows a large area of the Japanese archipelago, and the grey outline indicates the range of the map on the right. The map on the right shows UD (purple, 50%; blue, 75%; and light blue, 95%) of streaked shearwaters from 2011 to 2021. The black areas show the land topography. The oceanographic features of the Sea of Japan (SOJ) and the northwest Pacific Ocean (PO) are also shown in the figure. The white star indicates the location of the study site. b) Histograms of the trip duration (left) and total flight distance (right) of streaked shearwaters (purple, trips in the SOJ; light blue, trip in the PO). Details of recorded foraging trips are provided in chapter 4.

Chapter 3. Exhausted with foraging: Foraging behavior is related to oxidative stress in chick-rearing seabirds

3.1. Introduction

Foraging and provisioning efforts influence the reproductive performance of animals, and, in turn, their fitness. In diverse species (e.g., birds), parents must obtain food not only for themselves but also for their offspring during the offspring-rearing period. Such behavior is associated with physiological costs to parents, with potential trade-offs between current reproduction and self-maintenance for future reproduction (Stearns, 1989; Kaplan & Gangestad, 2015; Ogawa et al., 2015). Foraging behavior could lead to physiological deficits such as fatigue and pain, which could be mitigated by resting or obtaining nutrition (Zera & Harshman, 2001). Thus, investigating the physiological costs of foraging efforts of wild animals and how such costs potentially influence their foraging and provisioning behaviors could enhance the understanding of their foraging strategies and behavioral flexibility.

Oxidative stress has been reported to be one of the physiological costs associated with foraging and reproductive efforts (Costantini, 2008). Oxidative stress is induced by an imbalance between the levels of pro-oxidants and the capacity of antioxidants to neutralize pro-oxidants such as reactive oxygen species (ROS). ROS are produced by the reduction of oxygen molecules inhaled through respiration (Dröge, 2002). Although ROS can kill pathogens in tissues (Finkel, 2011), their excessive accumulation damages biomolecules such as DNA, proteins, and lipids (Skrip & Mcwilliams, 2016). In addition, accumulated ROS and oxidized biomolecules (pro-oxidants) cause muscular fatigue mainly due to the alteration of mitochondrial functions and an increase in the reliance on anaerobic pathways (Finaud & Filaire, 2006). Pro-oxidants are mitigated by antioxidants, including endogenous enzymes (e.g., superoxide dismutase), organic compounds (e.g., glutathione and uric acid), and extrinsic substances obtained from food (e.g., vitamins and carotenoids; Costantini, 2008) via repair of biomolecules and cells (Sun, 1990; Halliwell, 2011; Figure 3.1). Pro-oxidant levels in the body can be used as indices for fatigue, whereas antioxidant levels can be used as indices for the capability of tissues or the body to recover from fatigue.

Seabirds make foraging trips to feed both their offspring and themselves during the chick-rearing period. Oxidative stress negatively affects current and future reproduction in seabirds, e.g., first egg volume (Montoya et al., 2016), the number of chicks (Costantini & Dell'Omo, 2015), and future breeding probability (Costantini et al., 2015). Moreover, antioxidants derived from prey when foraging are likely to reduce the levels of pro-oxidants in seabirds (Beaulieu et al., 2010). Based on these previous findings, I hypothesize that oxidative stress is associated with foraging behavior, which potentially influences reproductive performance. However, to the best of my knowledge, no previous study has simultaneously explored foraging behavior and associated oxidative stress in wild seabirds.

In the present study, I evaluated the relationships between foraging behavior and oxidative stress in streaked shearwaters based on the following two hypotheses. The first hypothesis was that long-distance foraging trips and high physical activities may be related to their oxidative stress levels. The second hypothesis was that feeding activities may be related to their antioxidant levels owing to the intake of nutritional antioxidants. I used an integrative approach based on oxidative stress measurements (reactive oxygen metabolites, d-ROMs; biological antioxidant potential, BAP) and bio-logging techniques.

Concerning to the first hypothesis, long-distance foraging trips and high physical activity can increase pro-oxidant levels or decrease anti-oxidant levels in birds. In homing pigeons (*Columba livia*) individuals that take long flights exhibit increased pro-oxidant levels and decreased antioxidant levels compared to the levels at the pre-flight stage (Costantini et al., 2008). When shearwaters takeoff from the sea or the land surface, they must run or jump into the air and beat their wings rapidly to gain lift (Sato et al., 2009).

Takeoff, which is their most energy costly behavior (Weimerskirch et al., 2000; Sakamoto et al., 2013), could increase their oxidative stress. In addition, overall dynamic body acceleration (ODBA) calculated based on the acceleration data is often used to estimate energy expenditure under different behavioral modes (Qasem et al., 2012). As ODBA is related to metabolic rate and heart rates in free-living seabirds (Wilson et al., 2006; Hicks et al., 2017), it may also be associated with increased levels of oxidative stress.

Concerning to the second hypothesis, ODBA may decrease oxidative stress in birds as it includes foraging effort activities such as dives (Cianchetti-Benedetti et al., 2017). In free-living seabirds, prey containing antioxidant supplements increase antioxidant levels in plasma, likely reducing oxidative stress (carotenoids, Blount et al., 2002; vitamin E, Pérez et al., 2008) and antioxidant substances obtained from prey are likely to reduce their oxidative stress (Beaulieu et al., 2010). Fish, such as Japanese anchovy, which is the dominant prey of streaked shearwaters (Matsumoto et al., 2012), contains various vitamins (Science and Technology Agency, 2015); therefore, the levels of antioxidants in streaked shearwaters could increase because of their foraging efforts. In addition, high ODBA may increase oxidative stress in birds if they fail to obtain food for themselves and, alternatively, may decrease their oxidative stress if they obtain sufficient food for themselves.

3.2. Methods

3.2.1. Fieldwork and data collection

Adult streaked shearwaters were captured by hand and placed in opaque cloth bags. I collected blood samples within, on average, 7 min, and a maximum of 23 min after capture. A previous study reported no significant variations in pro-oxidant levels and total antioxidant capacity in the plasma during 30 min of retainment in wild songbirds

(Costantini et al., 2007). My short-term sampling procedure was less likely to increase the oxidative stress levels in captured birds.

To measure oxidative stress, I collected blood samples from the lower limb veins of the birds using a needle and syringe prefilled with a little anticoagulant heparin sodium (5000 unit/5 mL; Mochida Pharmaceutical Co., Ltd., Tokyo Japan). The samples were stored at ambient temperature (24.4 ◦C on average over the period from blood sampling to the end of the field experiment at night; temperature data at Awashima Island were obtained from the Japan Meteorological Agency) until transport to my research base. The volume of collected blood samples was less than 1 mL, corresponding to less than 1% of the streaked shearwaters' body masses. The blood samples were centrifuged at 2680 ×g for 10 min at room temperature within 6 h of blood collection. Blood cells and plasma were divided and stored frozen at −20 ◦C. In a previous study that carried out the same assay as mine (d-ROMs test and BAP test; details are described below), the levels of pro- and anti-oxidants in human plasma did not change significantly when the sample was left at room temperature (20–25 ◦C) for 30 min, 1 h, 2 h, 4 h, 6 h, and 8 h from blood collection until plasma separation (Nojima et al., 2010), suggesting that the levels of prooxidants and antioxidants in the present study remained stable over several hours of blood storage.

After the blood drawing procedures, GPS and acceleration data loggers (55 × 20 × 11 mm, 25.4 g; Axy-Trek, TechnoSmArt, Italy) were attached with the method described in chapter 2.2. The sampling intervals of the loggers were one fix per minute for GPS and 25 Hz for acceleration. Such settings allowed the loggers to record 13 days of data in 2018 and 17 days of data in 2019 at most. After 1 to 17 days of the logger attachment, I recaptured the birds and collected their blood samples, and retrieved the loggers. Blood samples were collected from each bird twice (i.e., when loggers were attached and retrieved). I also measured bill length, bill depth, head length, and tarsus length in 0.01 mm units using a digital caliper (CD-PS/PM; Mitutoyo Corporation, Kanagawa, Japan), and measured their wing lengths using a ruler in 1 mm units. In addition, I measured the body masses of each captured bird in 5 g units using a spring scale (Pesola LightLine

Metric 11,000%, ± 0.3%; PESOLA AG, Baar, Switzerland) each time a bird was captured. I recaptured 14 streaked shearwaters (six males and eight females) in 2018 and 20 streaked shearwaters (10 males and 10 females) in 2019 (Figure 3.2). Two birds captured in 2019 were the same birds captured in 2018 (one male and one female). The average recording duration of their behavior in 2018 was 8.5 days (ranging from 4 to 13 days) and in 2019 was 7.9 days (ranging from 1 to 17 days).

3.2.2. Measurements of pro-oxidant level and antioxidant capacity in plasma

Plasma pro-oxidant level was measured using the d-ROMs test and plasma antioxidant capacity was measured using the BAP test with a free radical analyzer (FREE Carrio Duo; Diacron International, Grosseto, Italy). The plasma concentrations of R-OOH (reactive oxygen metabolites; hydroperoxides; d-ROMs) were measured using the d-ROMs test and are expressed in Carratelli units (U. CARR = 0.08 mg H_2O_2/dL). The biological antioxidant potential (total antioxidant capacity in plasma; BAP), of endogenous organic compounds and extrinsic substances obtained from food, were measured in the BAP test. Before the experimental protocol was applied, the plasma was centrifuged at 17,765 ×g for 10 min at 4°C and stored at 4°C. The d-ROMs and BAP tests were conducted within 6 months of blood collection according to the experimental protocol. As a preliminary experiment, I measured the levels in 15 blood samples twice to confirm the reproducibility of the measurements obtained from the d-ROMs and BAP tests, revealing a small coefficient of variation of less than 5% on average (Table S3.1).

3.2.3. Data analyses and statistical analyses

From the GPS data, I defined foraging trips with method described in chapter 2.3. Foraging trip metrics such as trip durations, total flight distances, total maximum distance from the colony, and range of maximum distance from the colony were calculated from the data. The maximum distance from the colony was the maximum linear distance from the breeding site during each trip. The range of maximum distance from the colony was calculated by dividing the total maximum distance from the colony by the number of times of recorded foraging trips.

For evaluating the physical activity of the birds, total ODBA, average ODBA, the total number of takeoffs, and the average number of takeoffs were calculated using acceleration data. A high-pass filter (1.5 Hz; Watanuki et al., 2005) was applied to tri-axial acceleration data to remove the static component and, then, total ODBA was calculated by summing the high-pass filtered tri-axial acceleration data. To detect takeoff flapping and subsequent flight, I used the surge axis of acceleration data and the "Ethographer" (Sakamoto et al., 2009) package in IGOR Pro version 6.36 J (WaveMetrics Inc., OR, USA). The flight was defined as a series of movements from takeoff to a subsequent constant flight of more than 30 s. The number of flights, i.e., takeoffs, was counted based on the definition above. The body size index was calculated by principal components analysis for each year using the "prcomp" function in R. I used five parameters (bill length, bill depth, head length, tarsus length, and wing length), which remain constant during the breeding period. The first principal component (PC1) explained 59.0% and 66.5% of the variation in body size in 2018 and 2019, respectively.

To reveal the annual difference in foraging trip metrics, trip durations, total flight distances, and the maximum distance from the colony in each trip (Table S3.2), I constructed a generalized linear mixed model (GLMM) using the "glmer" function in the "lme4" package (Bates et al., 2022). Each foraging trip metric was used as a response variable, and sex and year were used as explanatory variables. Gamma distribution was used as the error structure and the link function "identity" was used. The individual was used as a random factor in the models. There was an annual difference in all the foraging trip metrics, trip durations ($t = -2.68$, $P = 0.01$), total flight distances ($t = -2.29$, $P = 0.022$), and the maximum distance from the colony ($t = -2.84$, $P = 0.00$). As there were significant annual differences in all foraging trip metrics for each trip, each year was analyzed separately in the subsequent analyses.

Changes in d-ROMs and BAP levels were calculated by subtracting the levels at the time of logger deployment from those at logger retrieval. To detect the sex-based differences in changes in d-ROMs levels, changes in BAP levels, foraging trip metrics, and level of physical activity, I performed the Wilcoxon rank-sum test for each year using the "wilcox.test" function in the "exactRankTests" package (Hothorn & Hornik., 2019).

To detect the linear relationship between oxidative stress (changes in d-ROMs and BAP levels) and foraging trip metrics (trip duration, total flight distance, total maximum distance from the colony, and range of maximum distance from the colony) and physical activities (total ODBA, average ODBA, the total number of takeoffs, and average number of takeoffs), I constructed a linear model (LM) for each using the "lm" function in R. To reveal the correlation between average ODBA and average number of takeoffs, I calculated the Pearson's product moment correlation coefficient using the "pearson" method in the "cor. test" function in R.

A generalized linear model (GLM) was constructed using the "glm" function in the "lme4" package to examine whether foraging behavior and sex were related to oxidative stress. The changes in d-ROMs and BAP levels were used as response variables, and trip duration, total flight distance, total maximum distance from the colony, range of maximum distance from the colony, total ODBA, average ODBA, total number of takeoffs, average number of takeoffs, and sex were used as explanatory variables. In addition, Gaussian distribution was used as the error structure and the link function "identity" was used. To avoid multi-collinearity, I removed the explanatory variable that had the highest variance inflation factor (VIF), not to exceed the threshold of 10 (Dormann et al., 2013). The VIF values were calculated using the "vif" function in the "car" package (Fox et al., 2020). The total trip duration, total maximum distance from the colony, total ODBA, and total number of takeoffs data were removed for 2018 and total flight distance, total maximum distance from the colony, total ODBA, and total number of takeoffs data were removed for 2019. Multicollinearity was not a problem as the VIF values of all parameters used in this analysis were less than 8 (Table S3.3). The model with the smallest Akaike’s Information Criterion (AIC) value was selected as the best model using the “stepAIC” function in the “MASS” (Ripley et al., 2020) package.

3.3. Results

3.3.1. Sex-based differences in oxidative stress and foraging behavior data

There were no sex-based differences in changes in d-ROMs levels, changes in BAP levels, foraging trip metrics, nor physical activities, although male body size (PC1) was significantly greater than female body size in both years (Table S3.4). There was a significant and positive correlation between average ODBA and average number of takeoffs in 2019 (t = 4.89, *P* = 0.00), and not in 2018 (t = 0.018, *P* = 0.99).

3.3.2. Relationship between foraging behavior and the changes in d-ROMs levels

Based on LM results, there was no significant relationship between foraging behavior and the changes in d-ROM levels in 2018 (Figure 3.3a, Figure 3.4a, Table S3.5), whereas the changes in d-ROMs levels were positively related to range of maximum distance from the colony (t = 2.38, *P* = 0.028; Figure 3.3b) and average number of takeoffs in 2019 (t = 2.18, *P* = 0.043; Figure 3.4b, Table S3.5).

The relationship between foraging behavior and the changes in d-ROMs levels was checked using the GLM. The null model was selected as the best model in 2018, whereas the model that included average number of takeoffs and sex as explanatory variables was selected as the best model in 2019. The changes in d-ROMs levels were positively related to average number of takeoffs in 2019 (t = 2.40, *P* = 0.028), and not in 2018 (Table S3.4).

3.3.3. Relationships between foraging behavior and the changes in BAP levels

Based on LM results, the changes in BAP levels were positively related to average ODBA in 2018 (t = 2.62, *P* = 0.023; Figure 3.4a, Table S3.6), whereas there was no significant relationship in 2019 (Figure 3.4b).

The relationships between foraging behavior and the changes in BAP levels were checked using the GLM. The model that included average ODBA as the explanatory variable was selected as the best model in 2018 and the null model was selected as the best model in 2019. The changes in BAP levels were positively related to average ODBA in 2018 (t = 2.62, *P* = 0.023), but not in 2019 (Table 3.1).

3.4. Discussion

To evaluate the stress responses of foraging behavior in streaked shearwaters during their chick-rearing period, I simultaneously recorded their behavior using bio-logging techniques and measured their oxidative stress. My results showed that neither the changes in d-ROMs nor BAP levels differed between the sexes, although male body size was significantly greater than female body size, as reported in previous studies (Shirai et al., 2013; Arima et al., 2014; Yamamoto et al., 2016a). However, I detected the following relationships between oxidative stress and foraging behavior.

Unlike in 2018, a positive relationship was observed between range of maximum distance from the colony and the changes in d-ROMs levels in 2019. The range of maximum distance from the colony in 2019 was more than two times that in 2018 (Figure 3.2), suggesting that long-range foraging trips might increase oxidative stress. Although some parents belonging to the order Procellariiformes obtain food and increase their body mass in areas distant from their colonies (Weimerskirch et al., 1997a; Weimerskirch et al., 2003; Congdon et al., 2005; Ochi et al., 2010), in the present study, long-distance flights from the colony neither decreased d-ROMs levels nor increased BAP levels in both years. Streaked shearwaters might not fly far from the colony to obtain food for themselves nor reduces their oxidative stress.

As expected, the average number of takeoffs was positively related to the changes in d-ROMs levels in 2019. In streaked shearwaters, frequent takeoffs increase metabolic rate, as calculated using the doubly labeled water (DLW) method (Shirai et al., 2012), in which carbon dioxide production and metabolic rate are estimated by injecting isotopes of oxygen and hydrogen (Lifson & McClintock, 1966; Speakman, 1997). Therefore, frequent takeoffs may lead to the accumulation of pro-oxidants by increasing metabolic rates of the birds. Shearwater and albatross wings have relatively high aspect ratios (i.e., long and narrow wings) compared to those of other birds (Warham, 1977); therefore, they can take long-distance flights (Denny, 2009); however, they must beat their wings rapidly to gain lift during the takeoff phases (Sato et al., 2009). Furthermore, in wandering albatrosses (*Diomedea exulans*) the heart rate during takeoff is faster than that during other behaviors (Weimerskirch et al., 2000), and frequent takeoffs increase their metabolic rate, as calculated based on the DLW method (Shaffer et al., 2001). In black-browed albatrosses (*Thalassarche melanophrys*) the estimated energy expenditure values during takeoffs are higher than those during other behaviors, such as landing and cruising flights (Sakamoto et al., 2013). High aspect ratio wings of such species might be more energy demanding during takeoffs, which could increase oxidative stress.

Average ODBA (i.e., a proxy for activity level) was positively related to the changes in BAP levels in 2018, suggesting that ODBA is associated with foraging efforts activities such as dives to obtain prey containing antioxidant substances in 2018. There was a significant and positive correlation between average ODBA and average number of takeoffs in 2019 (i.e., takeoff is directly linked to ODBA). However, no such significant correlation was observed in 2018, suggesting that they carried out high physical activity other than takeoffs, such as repeated dives or dipping from the sea surface, in 2018, rather than single plunge dives from the air. Although ODBA is positively related to oxygen consumption in several animals including seabirds (Halsey et al., 2009; Hicks et al., 2017), high ODBA might not always increase d-ROMs levels and may increase BAP levels via feeding on fish containing high amounts of antioxidant substances.

As mentioned previously, the relationship between the changes in oxidative stress and foraging behavior differed from year to year. In 2018, no significant relationship was observed between the average number of takeoffs and the changes in d-ROMs levels, probably because they could neutralize their oxidative stress associated with frequent takeoffs by antioxidant substances. In 2019, no significant relationship was observed between average ODBA and the changes in BAP levels. Average ODBA was positively correlated with average number of take-offs in 2019, and not in 2018, suggesting that streaked shearwaters often carried out single plunge dives from the air in 2019 and repeated dives or dipping from the sea surface after encountering a rich prey patch in 2018. Therefore, in 2019, streaked shearwaters experienced the cost of takeoffs after unsuccessful single plunge dives without the benefits of antioxidants provided by prey, since food availability was poor. The possibility of low food availability in 2019 was also observed since the individuals took longer foraging trips in 2019 than those in 2018 (Figure 3.2, Table S3.2). Streaked shearwaters might exploit distant foraging areas to compensate for low food availability, which had a negative consequence on their oxidative stress.

In summary, in 2019, d-ROMs levels increased with an increase in the range of maximum distance from the colony and the number of takeoffs; conversely, in 2018, BAP levels increased due to a higher level of possible feeding activity. However, such relationships were likely dependent on annually changing environmental conditions (i.e., food availability). Finally, I highlight that the combination of bio-logging and oxidative stress measurements can aid in evaluating the underlying physiological costs of the foraging behavior of wild animals. I also highlight that oxidative stress associated with foraging behavior and its annual difference in single trips could be related to how seabirds perform a sequence of multiple foraging trips such as the bimodal foraging strategy

(Chaurand &Weimerskirch, 1994; Weimerskirch et al., 1997a) and the flexible foraging strategy to adapt to the annually changing food supplies (Granadeiro et al., 1998).

3.5. Tables and figures

Table 3.1: Estimates of generalized linear model coefficients in 2018 and 2019. Δd-ROMs levels and ΔBAP levels were calculated by subtracting the levels at logger deployment from those at logger retrieval. d-ROMs; reactive oxygen metabolites, BAP; biological antioxidant potential, ODBA; overall dynamic body acceleration, *P*; P-value

Year	Response variable	Best model	Estimate	S. E.	*P*
2018	Δd-ROMs levels	Null model			
	ΔBAP levels	Intercept	-1221	430	0.015
		Average ODBA	0.042	0.016	0.023
2019	Δd-ROMs levels	Intercept	-82.18	41.67	0.065
		Average number of takeoffs	56.77	23.62	0.028
		Sex (Female)	-29.36	20.69	0.17
	ΔBAP levels	Null model			

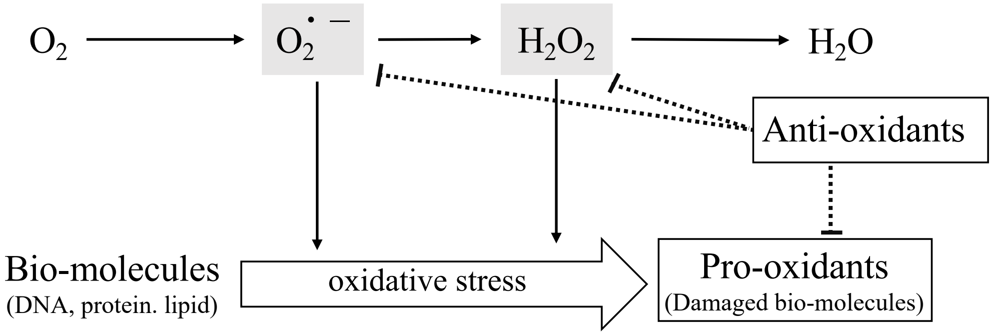


Figure 3.1: Overview of pro-oxidants and antioxidant capacity.

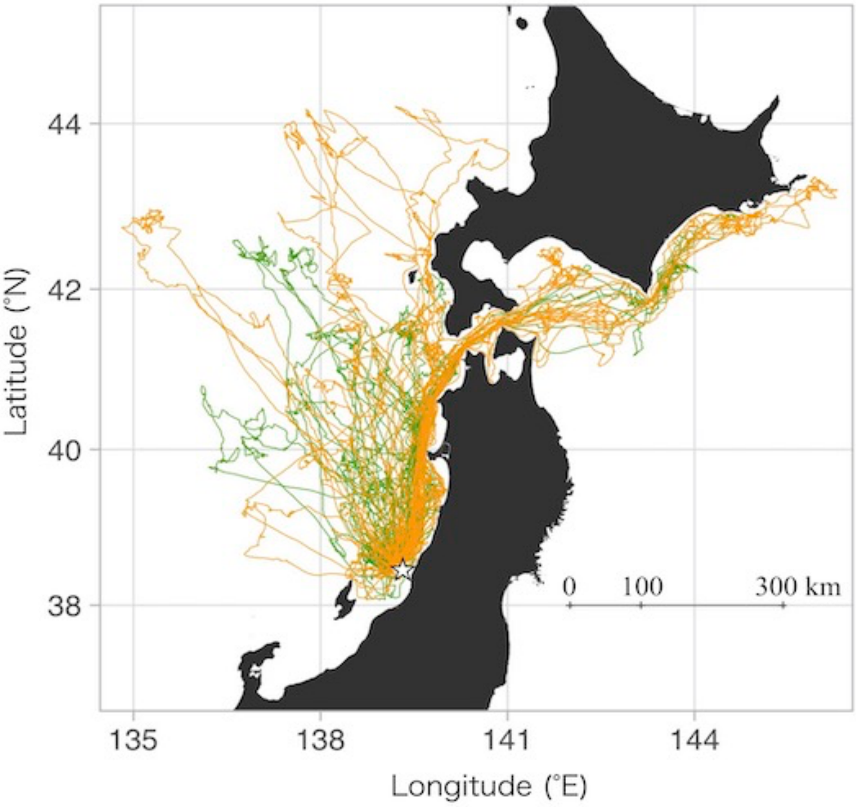


Figure 3.2: GPS trajectories of observed streaked shearwaters in 2018 (the number of recorded foraging trips = 55; green line) and 2019 (the number of recorded foraging trips = 48; yellow line). The star indicates the location of the study site. The black area shows the land topography.

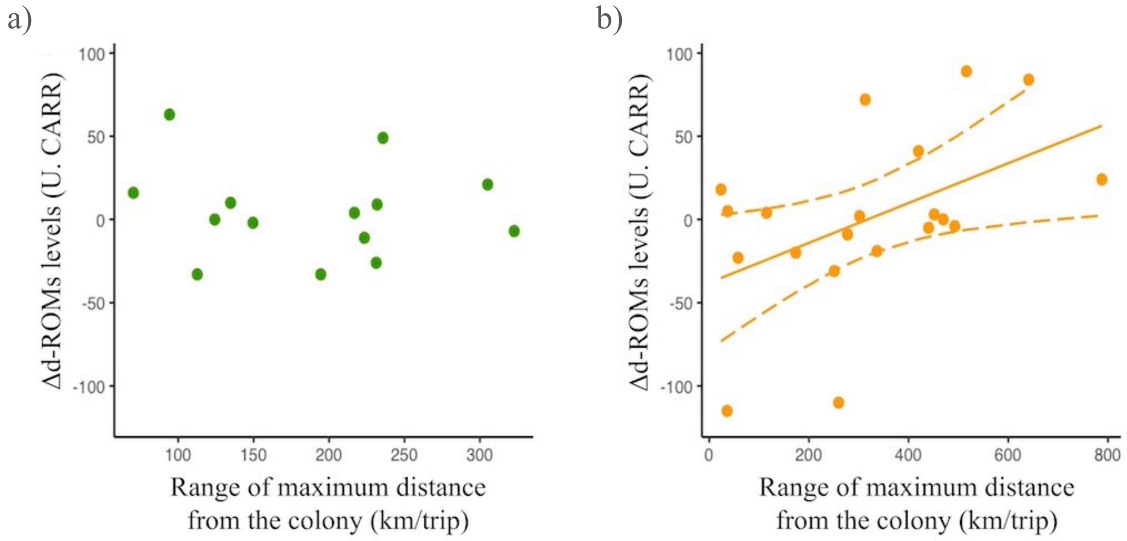


Figure 3.3: The relationship between the range of maximum distance from the colony per trip and changes in reactive oxygen metabolite (Δd-ROMs) levels in 2018 (a) and 2019 (b). In 2019, the changes in d-ROMs levels were positively related to the range of maximum distance from the colony per trip (b; solid yellow line; intercept = −38.00, slope = 0.12). Upper and lower dashed lines are 95% confidence intervals. The range of maximum distance from the colony was calculated by dividing total maximum distance from the colony with the number of times of recording foraging trips. The Δd-ROMs levels were calculated by subtracting the levels at logger deployment from those at logger retrieval.

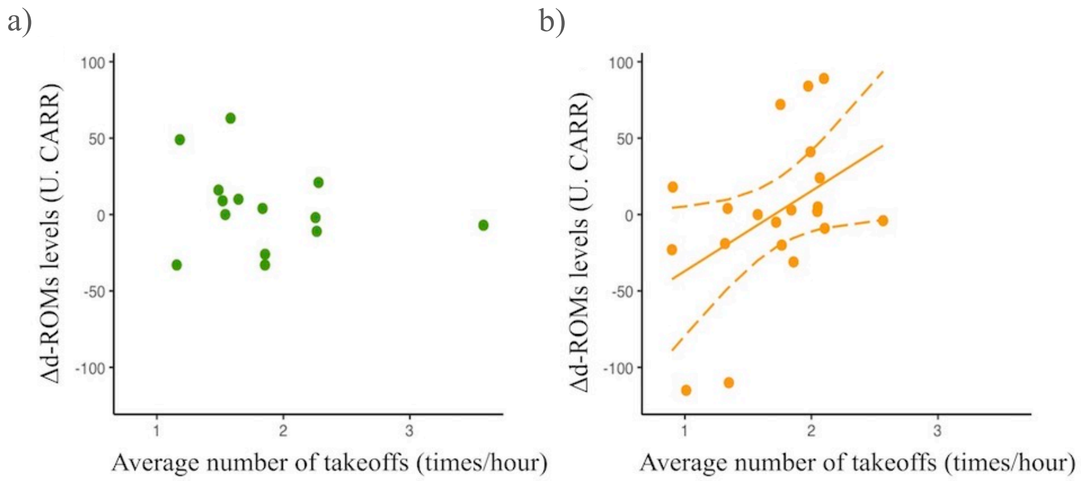


Figure 3.4: The relationship between the average number of takeoffs and changes in reactive oxygen metabolite (Δd-ROMs) levels in 2018 (a) and 2019 (b). In 2019, the changes in d-ROMs level were positively related to average number of takeoffs (b; solid yellow line; intercept = −89.29, slope = 52.35). Upper and lower dashed lines are 95% confidence intervals. The Δd-ROMs levels were calculated by subtracting the levels at logger deployment from those at logger retrieval.

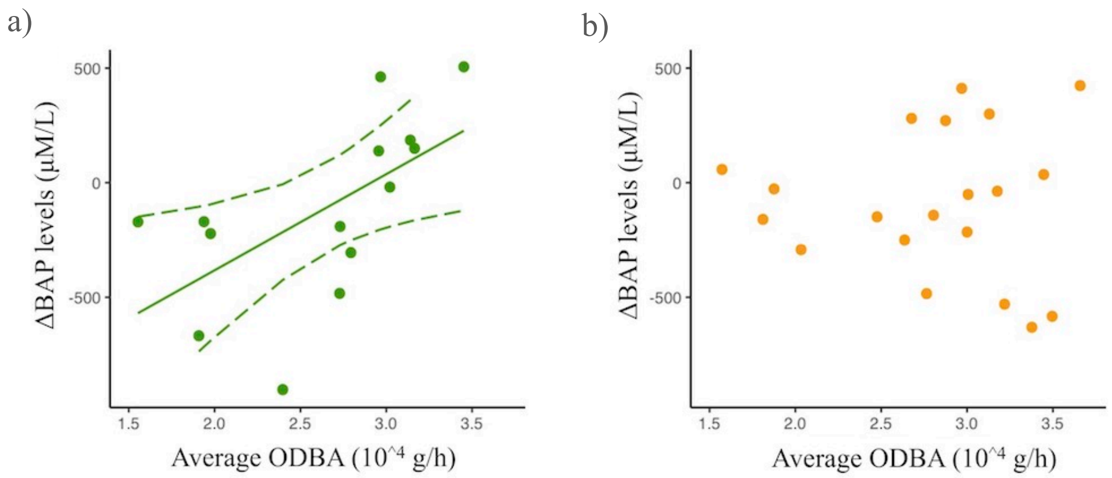


Figure 3.5: The relationship between average overall dynamic body acceleration (ODBA) and changes in biological antioxidant potential (ΔBAP) levels in 2018 (a) and 2019 (b). In 2018, the changes in BAP level were positively related to the average ODBA (a; solid green line; intercept = −1221, slope = 419.4). Upper and lower dashed lines are 95% confidence intervals. The ΔBAP levels were calculated by subtracting the levels at logger deployment from those at logger retrieval.

3.6. Appendices

3.6.1 Appendices method

Changes in body masses were calculated by subtracting the value at logger deployment from those at logger retrieval. To examine the relationship between the changes in oxidative stress (the d-ROMs levels and the BAP levels) and the changes in body masses, a linear model (LM) was constructed by using the “lm” function in R.

To detect the year differences in changes in d-ROMs levels and changes in BAP levels, I performed the Wilcoxon rank-sum test for each year using the “wilcox_test” function in the “coin” package (Hothorn et al., 2021).

3.6.2 Appendices results

Changes in d-ROMs levels significantly and positively related to the changes in body masses ($t = 2.20$, $P = 0.048$; Figure S3.1a). Changes in BAP levels were significantly and negatively related to the changes in body masses ($t = -2.32$, $P = 0.039$; Figure S3.1b) in 2018; however, no such relationship was detected in 2019 ($t = -0.76$, $P = 0.46$; Figure S3.1c; $t = -0.92$, $P = 0.37$; Figure S3.1d).

There was no significant year difference in changes in d-ROMs levels ($z = 0.07$, $P = 0.95$) nor changes in BAP levels ($z = -0.25$, $P = 0.82$).

Table S3.1: Reproducibility of d-ROMs and BAP measurements. Units of d-ROMs and BAP are U. CARR and µM/L respectively. SD; standard deviation, CV; coefficient of variation.

	d-ROMs					BAP				
ID	1st	2nd	Average	SD	CV (%)	1st	2nd	Average	SD	CV (%)
1	71	75	73	2.83	3.87	1979	1925	1952	38.18	1.96
2	87	92	89.5	3.54	3.95	2207	2204	2205.5	2.12	0.10
3	77	78	77.5	0.71	0.91	1689	1764	1726.5	53.03	3.07
4	73	76	74.5	2.12	2.85	2085	2017	2051	48.08	2.34
5	114	121	117.5	4.95	4.21	1644	1533	1588.5	78.49	4.94
6	80	81	80.5	0.71	0.88	1788	1730	1759	41.01	2.33
7	78	84	81	4.24	5.24	1483	1401	1442	57.98	4.02
8	150	158	154	5.66	3.67	1304	1241	1272.5	44.55	3.50
9	101	107	104	4.24	4.08	1311	1599	1455	203.65	14.00
10	23	30	26.5	4.95	18.68	1905	1839	1872	46.67	2.49
11	44	47	45.5	2.12	4.66	1719	1682	1700.5	26.16	1.54
12	98	87	92.5	7.78	8.41	1490	1588	1539	69.30	4.50
13	85	81	83	2.83	3.41	1400	1388	1394	8.49	0.61
14	49	50	49.5	0.71	1.43	1318	1423	1370.5	74.25	5.42
15	50	46	48	2.83	5.89	1417	1441	1429	16.97	1.19

Table S3.2: Trip durations, total flight distances, and the maximum foraging range in each trip of the observed streaked shearwaters; average (minimum–maximum).

Year	Sex (trip No.)	Trip duration (d)	Total flight distance (km)	Maximum distance (km)
2018	Male (27)	1.69 (1–6)	585.61 (52–2086)	178.65 (15–674)
	Female (28)	1.93 (1–8)	681.14 (128–2689)	162.00 (35–577)
2019	Male (25)	2.80 (1–8)	1033.23 (82–3125)	320.86 (23–794)
	Female (23)	3.12 (1–8)	984.62 (27–2340)	275.95 (11–646)

Table S3.3: The variance inflation factor (VIF) values of all parameters used as explanatory variables in the GLM were less than 8 in the present study. ODBA; overall dynamic body acceleration

Year	Explanatory variables	VIF
2018	Total flight distance	2.03
	Range of maximum distance from the colony	2.73
	Average number of takeoffs	1.84
	Average ODBA	1.12
	Sex	1.24
2019	Total trip duration	1.91
	Range of maximum distance from the colony	3.54
	Average number of takeoffs	2.39
	Average ODBA	7.23
	Sex	1.23

Table S3.4: Sex-based data of oxidative stress, foraging behavior, and body mass data of streaked shearwaters in 2018 (a) and 2019 (b; average ± SD). Δd-ROMs levels and ΔBAP levels were calculated by subtracting the levels at logger deployment from those at logger retrieval. Total maximum distance was calculated by summing the maximum distance from the colony for each trip. Range of maximum distance was calculated by dividing total maximum distance covered by the number of times of recorded foraging trips. d-ROMs; reactive oxygen metabolites, BAP; biological antioxidant potential, ODBA; overall dynamic body acceleration, P; P-value.

a) 2018	Male	Female	W	P
Δd-ROMs levels (U. CARR)	-1.2 ± 30	8.4 ± 27	18	0.44
ΔBAP levels (μM/L)	-98 ± 344	-138 ± 460	21	0.75
Total trip duration (h)	183 ± 67	163 ± 56	28	0.66
Total flight distance (km)	2636 ± 993	2385 ± 709	27	0.75
Total maximum distance (km)	730 ± 367	626 ± 147	25	0.95
Range of maximum distance (km/trip)	170 ± 70	203 ± 83	20	0.66
Total ODBA (10^4 g)	596 ± 176	509 ± 240	30	0.49
Average ODBA (10^4 g/h)	2.7 ± 0.4	2.5 ± 0.7	27	0.75
Total number of takeoffs (times)	394 ± 144	355 ± 164	28	0.66
Average number of takeoffs (times/h)	1.8 ± 0.4	1.9 ± 0.8	26	0.85
Body size (PC1)	1.4 ± 1.7	-1.1 ± 0.7	46	<0.001
Δbody masses (g)	-45 ± 38	-21 ± 31	17	0.40

b) 2019	Male	Female	W	P
Δd-ROMs levels (U. CARR)	12 ± 30	-11 ± 67	68	0.19
ΔBAP levels (µM/L)	-103 ± 381	-74 ± 269	50	1
Total trip duration (h)	156 ± 123	188 ± 105	43	0.63
Total flight distance (km)	2377 ± 2022	2463 ± 1322	45	0.74
Total maximum distance (km)	739 ± 657	691 ± 390	50	1
Range of maximum distance (km/h)	320 ± 256	320 ± 169	51	0.97
Total ODBA (10^4 g)	517 ± 445	623 ± 369	30	0.63
Average ODBA (10^4 g/h)	2.7 ± 0.7	2.9 ± 0.4	40	0.48
Total number of takeoffs (times)	318 ± 272	371 ± 224	43	0.63
Average number of takeoffs (times/h)	1.7 ± 0.5	1.8 ± 0.4	45	0.74
Body size (PC1)	1.6 ± 0.7	-1.6 ± 0.7	100	<0.001
Δbody masses (g)	-29 ± 47	-8.5 ± 26	35	0.26

Table S3.5: Estimates of linear model coefficients for the relationships between the changes in reactive oxygen metabolite (Δd-ROMs) levels and the foraging behavior in streaked shearwaters in 2018 (a) and 2019 (b).

a) 2018	Explanatory variables	Estimate	S. E.	P
Δd-ROMs levels	Intercept	14.72	24.34	0.56
	Total trip duration	-0.061	0.13	0.66
	Intercept	16.17	25.43	0.54
	Total flight distance	-0.0048	0.01	0.63
	Intercept	14.86	22.05	0.53
	Total maximum distance	-0.016	0.031	0.62
	Intercept	12.13	21.06	0.58
	Range of maximum distance	-0.042	0.10	0.70
	Intercept	9.73	22.1	0.67
	Total ODBA	-9.95×10^{-7}	3.77×10^{-6}	0.8
	Intercept	15.8	37.3	0.68
	Average ODBA	-4.37×10^{-4}	-1.39×10^{-3}	0.76
	Intercept	20.29	20.59	0.34
	Total number of takeoffs	-0.043	0.052	0.42
	Intercept	22.14	24.93	0.39
	Average number of takeoffs	-9.60	12.78	0.47

b) 2019	Explanatory variables	Estimate	S. E.	P
Δd-ROMs levels	Intercept	-14.16	21.69	0.52
	Total trip duration	0.084	0.11	0.44
	Intercept	-20.60	20.44	0.33
	Total flight distance	0.0086	0.0070	0.23
	Intercept	-18.78	19.54	0.55
	Total maximum distance	0.027	0.022	0.25
	Intercept	-38.00	19.10	0.062
	Range of maximum distance	0.12	0.050	0.028
	Intercept	-15.97	20.41	0.44
	Total ODBA	-2.85×10^{-6}	-2.95×10^{-6}	0.35
	Intercept	-97.39	54.06	0.088
	Average ODBA	0.0035	0.0019	0.082
	Intercept	-19.2	20.07	0.35
	Total number of takeoffs	0.057	0.048	0.25
	Intercept	-89.29	42.51	0.05
	Average number of takeoffs	52.35	24.07	0.043

Table S3.6: Estimates of linear model coefficients for the relationships between the changes in biological antioxidant potential levels (ΔBAP) levels and the foraging behavior in streaked shearwaters in 2018 (a) and. 2019 (b).

a) 2018	Explanatory variables	Estimate	S. E.	P
ΔBAP levels	Intercept	-525	331	0.14
	Total trip duration	2.36	1.83	0.22
	Intercept	-482	353	0.2
	Total flight distance	0.14	0.13	0.3
	Intercept	-197	320	0.55
	Total maximum distance	0.11	0.45	0.8
	Intercept	-444	288	0.15
	Range of maximum distance	1.71	1.42	0.25
	Intercept	-643	274	0.037
	Total ODBA	-9.55×10^{-5}	-4.69×10^{-5}	0.065
	Intercept	-1221	430	0.015
	Average ODBA	0.042	0.016	0.023
	Intercept	-290	300	0.35
	Total number of takeoffs	0.46	0.75	0.56
	Intercept	-165	367	0.66
	Average number of takeoffs	23.93	188	0.90

b) 2019	Explanatory variables	Estimate	S. E.	P
ΔBAP levels	Intercept	-50.24	137	0.72
	Total trip duration	-0.22	0.67	0.75
	Intercept	-25.16	131	0.85
	Total flight distance	-0.026	0.045	0.57
	Intercept	-53.28	126	0.68
	Total maximum distance	-0.049	0.14	0.74
	Intercept	-114	136	0.41
	Range of maximum distance	0.08	0.36	0.83
	Intercept	-42.51	130	0.75
	Total ODBA	-8.06×10^{-6}	1.88×10^{-5}	0.67
	Intercept	-56.31	367	0.88
	Average ODBA	0.00	0.013	0.93
	Intercept	-43.60	129	0.74
	Total number of takeoffs	-0.13	0.31	0.68
	Intercept	-38.82	297	0.90
	Average number of takeoffs	-29.00	168	0.87

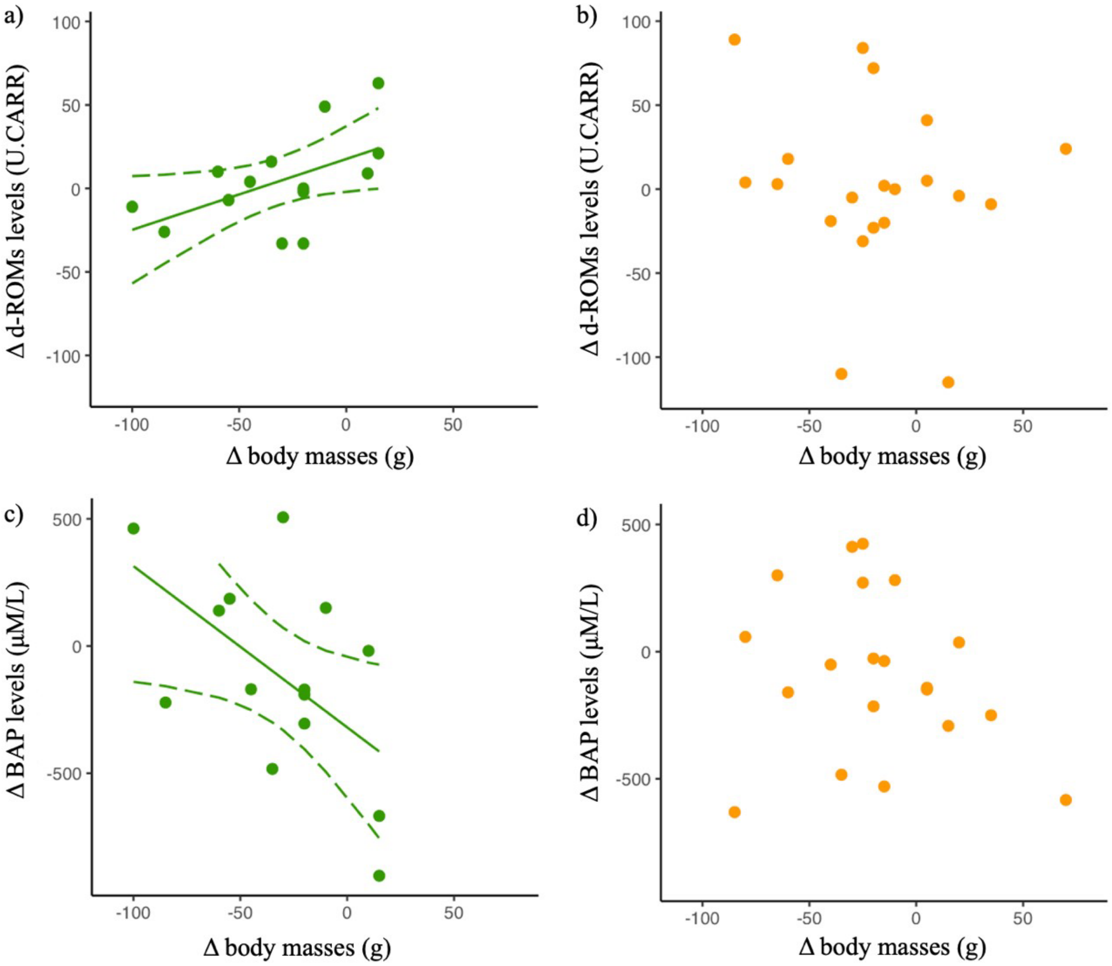


Figure S3.1: Changes reactive oxygen metabolite (Δd-ROMs) levels (a and b) and biological antioxidant potential (ΔBAP) levels (c and d) in relation to the changes in body masses in 2018 (Δbody masses; a and c) and 2019 (b and d). In 2018, the changes in body masses were significantly and positively related to the changes in d-ROMs levels (solid green line; intercept = 17.61, slope = 0.4239), and negatively related to the changes in BAP levels (solid green line; intercept = -319.80, slope = -6.337). Dashed lines show 95% confidence interval. Δd-ROMs levels, ΔBAP levels, and Δbody masses were calculated by subtracting the levels at logger deployment from those at logger retrieval.

Chapter 4. Interspecific associations among marine top predators in the air-sea boundary layer at local and large spatial scales

4.1. introduction

Interspecific relationships (such as competition and forging) are key in determining the distribution of wild animals and the structure of ecosystem dynamics (Chase et al., 2002). The distribution of top predators that have a significant impact on ecosystems (Estes, 1996; Schmitz et al., 2010) is likely to be determined by distribution and occurrence of their prey species and those of other predators, which share the same prey species (Hunt, 1990; Abrams, 2010). However, the knowledge of the interspecific relationships among marine top predators is still limited in comparison to that of terrestrial animals.

At the air-sea boundary layer, marine top predators aggregate in the air and underwater in anticipation of a feast from air and underwater and may induce positive interactions, resulting in high foraging success at a local spatial scale (Evans, 1982; Maxwell & Morgan, 2013). Among them, seabirds are highly mobile and are assumed to adapt a foraging strategy called local enhancement, which uses other predators, such as marine mammals and large fish, as cues for prey location (Silverman et al., 2004; Hebshi et al., 2008; Thiebot & Weimerskirch, 2013; Thiebault et al., 2014; Tremblay et al., 2014; Veit & Harrison, 2017; Garrod et al., 2021). Thus, seabird distribution is expected to reflect interspecific interactions with aquatic predators at a local spatial scale, resulting in large scale interspecific interactions. However, knowledge of seabird distribution in relation to that of other predators of the same prey species is scarce, resulting in a limited understanding of interactions, especially at a large scale.

Here, I examined instantaneous and long-term relationships in behavior and distribution between streaked shearwaters and common dolphinfish (*Coryphaena hippuru*) by deploying video loggers or GPS loggers on individual shearwaters. These two species potentially compete for prey, such as Japanese anchovy, in East Asia (Kojima, 1966; Matsumoto et al., 2012). Streaked shearwaters conduct shallow dives, most of which are shallower than 3 m and lasted 2–6 s, to forage fish on the sea surface during the day (Matsumoto et al., 2012). The common dolphinfish, which is a tropical and subtropical marine fish species, is found at a 5 m depth for approximately 80% of daytime (Lin et al., 2020). Streaked shearwaters breeding in the Pacific Ocean have been shown to increase their foraging intensity in the presence of other large predators, including common dolphinfish (Garrod et al., 2021). Therefore, streaked shearwaters are expected to forage with local enhancement and share Japanese anchovy schools with common dolphinfish in the air-sea boundary layer. I hypothesized that 1) the predators distribute themselves according to their prey (Davoren, 2000; Davoren et al., 2003; Ainley et al., 2009; Torres, 2009; Green et al., 2015), that is, in years when the anchovy stock is low, streaked shearwaters will fly farther from the colony and the dolphinfish stock would also be low; and 2) the predators would show positive relationships, that is, in years when the dolphinfish stock is high, the shearwaters associated with the dolphinfish will travel longer and father from the colony.

4.2 Method

4.2.1 Fieldwork

Fieldwork was conducted every year from 2011 to 2021. Animal-borne GPS loggers (GiPSy-2, 37×16×4 mm; GiPSy-4, 37×19×6 mm; or Axy-Trek, Technosmart, Roma, Italy) were attached with method described in chapter 2.2, or a harness using a Teflon ribbon (TH-25; width, 6 mm; BallyRibbonMills, Bally, Pennsylvania, USA) and recorded GPS positions approximately two weeks. The GiPSy-type loggers were housed in waterproof heat-shrink tubing. Another GPS logger (PinPoint VHF; 18 g, Lotek Wireless Inc., Newmarket, Ontario, Canada) was attached with a body harness to record birds' positions until the end of the breeding period. All loggers recorded GPS positions more than 1 point per 5 min (detailed in Table S4.1). To obtain direct evidence that the shearwaters, dolphinfish, and Japanese anchovy interact in the SOJ, I obtained video data of foraging scenes from 15 streaked shearwaters (one in 2019, five in 2020, three in 2021, and six in 2022) was obtained using animal-borne video loggers attached with method described in chapter 2.2.

4.2.2 Analyses of GPS data

From the GPS data, I removed low accuracy data, defined foraging trips, and the interpolated missing values with method described in chapter 2.3. These selected trips were classified into two groups: trips where the birds crossed (assigned as 1) a straight boundary line connecting two points on east side of the Tsugaru Strait (38°28′ N, 139°14′ E and 41 °48′N, 141°11′ E) or not (assigned as 0). For each foraging trip in which the birds did not cross the boundary line, the trip duration in the SOJ was calculated.

In the later analyses, I used yearly average of trip duration in the SOJ. In obtaining these yearly averages, it is desirable to remove the effect of individual variation rather than taking a simple yearly average because the trip data includes trips of the same individual, either in the same year and/or across years. To this end, I applied GLMM for each variable, with them as response variables, year as a categorical explanatory variable, and individual ID as a random effect, and then, the mean value of each variable for each year were estimated (Table S4.2). The trip duration was log-transformed, and a normal distribution was used as the probability distribution.

4.2.3 Bayesian statistical to estimate annual catch mass of fish in the SOJ

In the semi-closed SOJ, common dolphinfish and Japanese anchovy are targeted by fisheries using several different types of fishing gear. Among them, fixed nets are suitable for quantifying annual fluctuations in fish biomass because they are passive gear that catch migratory fish entering into the net; therefore, its fishing efforts remains relatively unchanged (Hubert et al., 2012). In addition, the annual fluctuations in catches at different ports in the SOJ varied simultaneously (Figure S4.1), suggesting that the Tsushima Warm Current, the dominant current flowing south to north in the SOJ, drives the distribution of anchovy and dolphinfish. This synchrony provides a plausible justification for estimate the yearly abundance of common dolphinfish and Japanese anchovy in the SOJ by Bayesian statistical inference using a fixed-net (mass) dataset from four different areas in the SOJ.

I obtained the catch data for common dolphinfish and Japanese anchovy from SOJ prefectures in September from 2011 to 2021. These two species were caught using fixed-net fishing method with almost constant fishing effort for each year. The catch data were obtained for Japanese anchovy and common dolphinfish from three prefectures (Toyama, Fukui, and Kyoto) and four prefectures (Akita, Toyama, Fukui, and Kyoto; Figure S4.2a), respectively. I defined the variable "abundance" as a proxy for the annual catch mass of Japanese anchovy and common dolphinfish in the SOJ. Abundance is a measure of the extent to which the common trend in catch mass for all prefectures differs among years. The catch mass in a given year for each prefecture was defined as the abundance for that year multiplied by a prefecture-specific constant (which is independent of the year). Specifically, the catch mass in year *t* (= 2011,2012,...,2021) of species *i* (= anchovy, dolphinfish) in prefecture *j* (= Fukui, Toyama, Kyoto, and Akita), represented by $c_{i,t,j}$, was defined as the abundance of species *i* in the year t ($a_{i,t}$) multiplied by the prefecture-specific constant $B_{i,j}$, as shown by Equation 1,

$$c_{i,t,j} \sim B_{i,j} \mathcal{N}\left(a_{i,t}, \sigma_i\right) \tag{1}$$

The σ_i represents the standard deviation of the abundance of species i. For standardization, I imposed a simplex condition was imposed on $a_{i,t}$ ($\sum_{t=2011}^{2022} a_{i,t} = 1$). This hierarchical Bayesian model was implemented in RStan and applied to the catch mass data to estimate the abundance of Japanese anchovy and common dolphinfish in each year. In this model, four Markov chain Monte Carlo (MCMC) chains were run for 10,000 iterations, discarding the first 1,000 samples for each chain. Convergence was evaluated when the R-hat value for each parameter was less than 1.1 (Table S4.3 and S4.4).

3.2.4 hierarchical Bayesian modelling

I then examined the effects of the estimated abundance of common dolphinfish and Japanese anchovy on the trip duration of streaked shearwaters. Here, I considered the confounding effect of Japanese anchovy abundance on common dolphinfish abundance. Specifically, I assumed the following linear model 2 and 3:

$$a_{\mathrm{dolphinfish},t} \sim \mathcal{N}\left(d_1 + d_2 a_{\mathrm{anchovy},t}, \rho_{\mathrm{dolphinfish}}\right) \tag{2}$$

$$s_t \sim \mathcal{N}\left(e_1 + e_2 a_{\mathrm{anchovy},t} + e_3 a_{\mathrm{dolphinfish},t}, \rho_{\mathrm{s}}\right) \tag{3}$$

where s_t represents the mean trip duration of streaked shearwaters in year t obtained from GPS data. The regression coefficients are represented by d_1, d_2, e_1, e_2, and e_3, whereby d_2 is the effect of Japanese anchovy abundance on that of common dolphinfish, e_2 is the effect of Japanese anchovy abundance on the trip duration of streaked shearwaters, and e_3 is the effect of common dolphinfish abundance on the trip duration of streaked shearwaters. $\rho_{\mathrm{dolphinfish}}$ and ρ_{s} are the standard deviations.

In this model, four MCMC chains were run for 10,000 iterations, discarding the first 1,000 samples for each chain. Convergence was evaluated when the R-hat value for each parameter was less than 1.1 (Table S4.5).

4.3 Result

Using video loggers, I obtained direct evidence of interactions between streaked shearwaters, common dolphinfish, and small fish schools, which were assumed to be

Japanese anchovy (Figure 4.1, Appendix Figure S4.2b). The instantaneous coexistence of streaked shearwaters and common dolphinfish was the same as that in a previous study in the Pacific Ocean (Garrod et al., 2021). I succeeded in recording attacks on school of small fish by streaked shearwaters from the air and common dolphinfish from below the water (Figure 4.1b and 4.1c). In all five videos with common dolphinfish (two in 2020, one in 2021, two in 2022), they did not chase or attack streaked shearwaters. In four of the five videos with common dolphinfish (two in 2020, one in 2021, one in 2022), schools of small fish, possible Japanese anchovy, were also recorded. In one video from 2022, one common dolphinfish was observed below a diving streaked shearwater, but there was no recordings of streaked shearwaters foraging on common dolphinfish. My results indicate that streaked shearwaters might forage more efficiently with the help of common dolphinfish that chase small fish to the sea surface (Veit & Harrison, 2017; Garrod et al., 2021).

Subsequently, from the decadal data of GPS loggers, 2,183 foraging trips from 414 streaked shearwaters (265 individuals) in the middle of August to the end of September from 2011 to 2021 were analyzed. The trip duration of streaked shearwaters in the SOJ was positively correlated with the estimated abundance of common dolphinfish (coefficient = 2.77), which was negatively correlated with that of Japanese anchovy (coefficient = -0.43); although, the estimated abundance of Japanese anchovy was not correlated with the trip duration of streaked shearwaters (Figure 4.2; Figure S4.3). This indicates that streaked shearwaters fly for longer duration in years when common dolphinfish were abundant and Japanese anchovy are scarce in the SOJ. However, a scarcity of Japanese anchovy was not found to directly relate to longer flights by streaked shearwaters.

4.4 Discussion

In contrast to the first hypothesis that predators are expected to distribute themselves according to their prey, no relationship existed between the distributions of streaked shearwaters and Japanese anchovy, whereas a negative relationship was discovered between the distributions of common dolphinfish and Japanese anchovy. It indicated that streaked shearwaters might switch their prey from Japanese anchovy to other species such as Japanese sardine (*Sardinops melanostictus*; Kurasawa et al., 2012) and bullet mackerel (personal communication, Yamamoto), rather than extending their foraging trips to compensate for the scarcity of Japanese anchovy. The negative relationship of Japanese anchovy abundance with common dolphinfish might show that a high abundance of common dolphinfish, which prefer relatively high temperature (SST over 20°C; Lin et al., 2020), indicate an environment disfavored by Japanese anchovy, which prefer relatively low temperature (SST in offshore area ranged 8–24°C; Takasuka et al., 2005).

As expected in the second hypothesis, streaked shearwaters flew for longer periods of time when associated with dolphinfish abundance in the SOJ. Although it is challenging to quantify the distribution of migrating fish species, abundant common dolphinfish might indicate their northward movement associated with the northward flow of the Tsushima Warm Current, potentially driving streaked shearwaters northward following common dolphinfish which is a cue of shearwaters' prey (Veit & Harrison, 2017), resulting in longer foraging trips. Streaked shearwaters might forage in association with other predators from the air-sea boundary, such as common dolphinfish, more often than would be expected by chance, has been observed locally in other seabirds (Hebshi et al., 2008; Thiebot & Weimerskirch, 2013; Garrod et al., 2021). Seabirds may forage according to their association with other predators from the sea, and this association might shape not only their local distribution but also their large-scale distribution.

Streaked shearwaters flew farther in years when common dolphinfish abundance was high, which did not exclude the possibility that streaked shearwaters might avoid foraging in areas where common dolphinfish occurred. This was supported by video observations where common dolphinfish appeared to accidentally block streaked shearwaters from reaching Japanese anchovies (Figure 4.1d).

To summarize, I demonstrated novel interspecific positive relationships among top predators from the air-sea boundaries on both instantaneous and long-term scales. My results indicate that the large-scale foraging behavior of seabirds is related to other predators from the air-sea boundary, not to the abundance of their dominant prey.

4.5. Figures

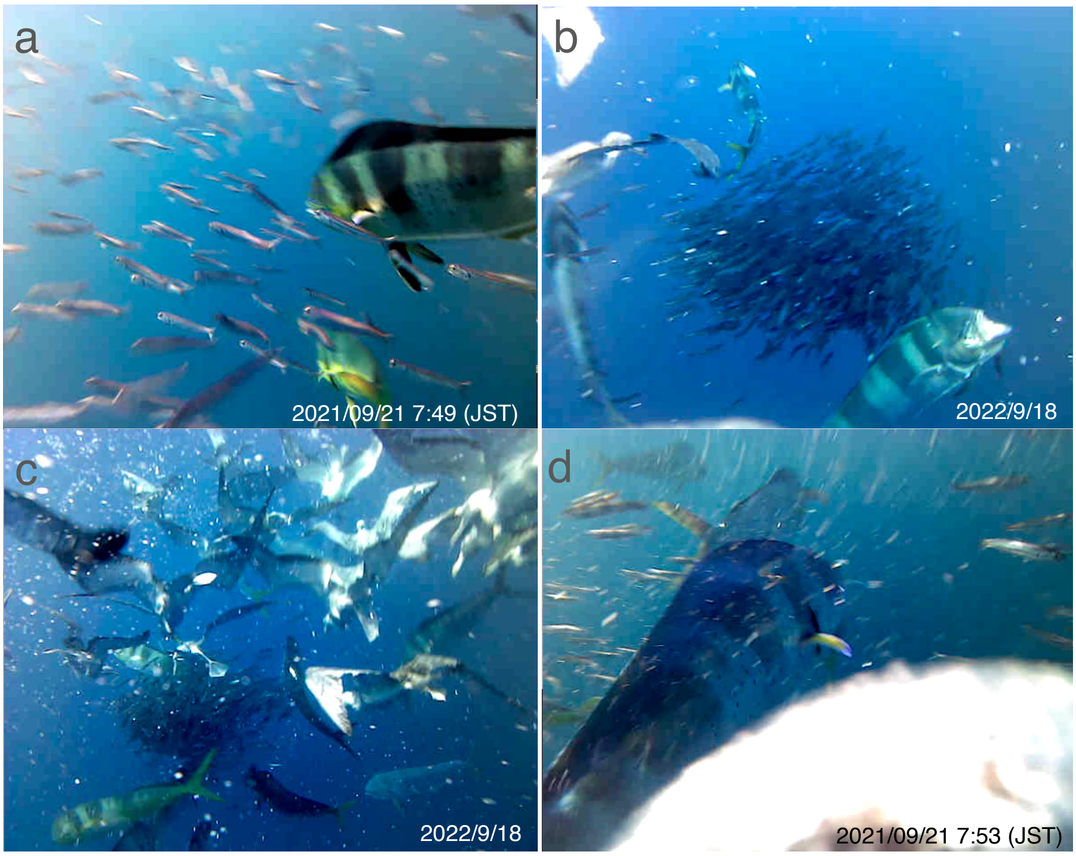


Figure 4.1: Screenshots from the video logger. Images (a) and (d) were taken at 7:49 and 7:53 am, respectively, on September 21st, 2021 (local time, JST) at 40°24′ N, 139°51′ E. Images (b) and (c) were taken at approximately 12:00 noon on September 18th, 2022 (local time, JST) at approximately 39°16′ N, 139°13′ E (the video logger failed to record accurate timings and locations). Image (a) displays the common dolphinfish and possible Japanese anchovy. In images (b) and (c), streaked shearwaters are seen diving into the sea as common dolphinfish chase fish schools. In image (d), the head of a common dolphinfish (bottom of image) is seen blocking the streaked shearwater.

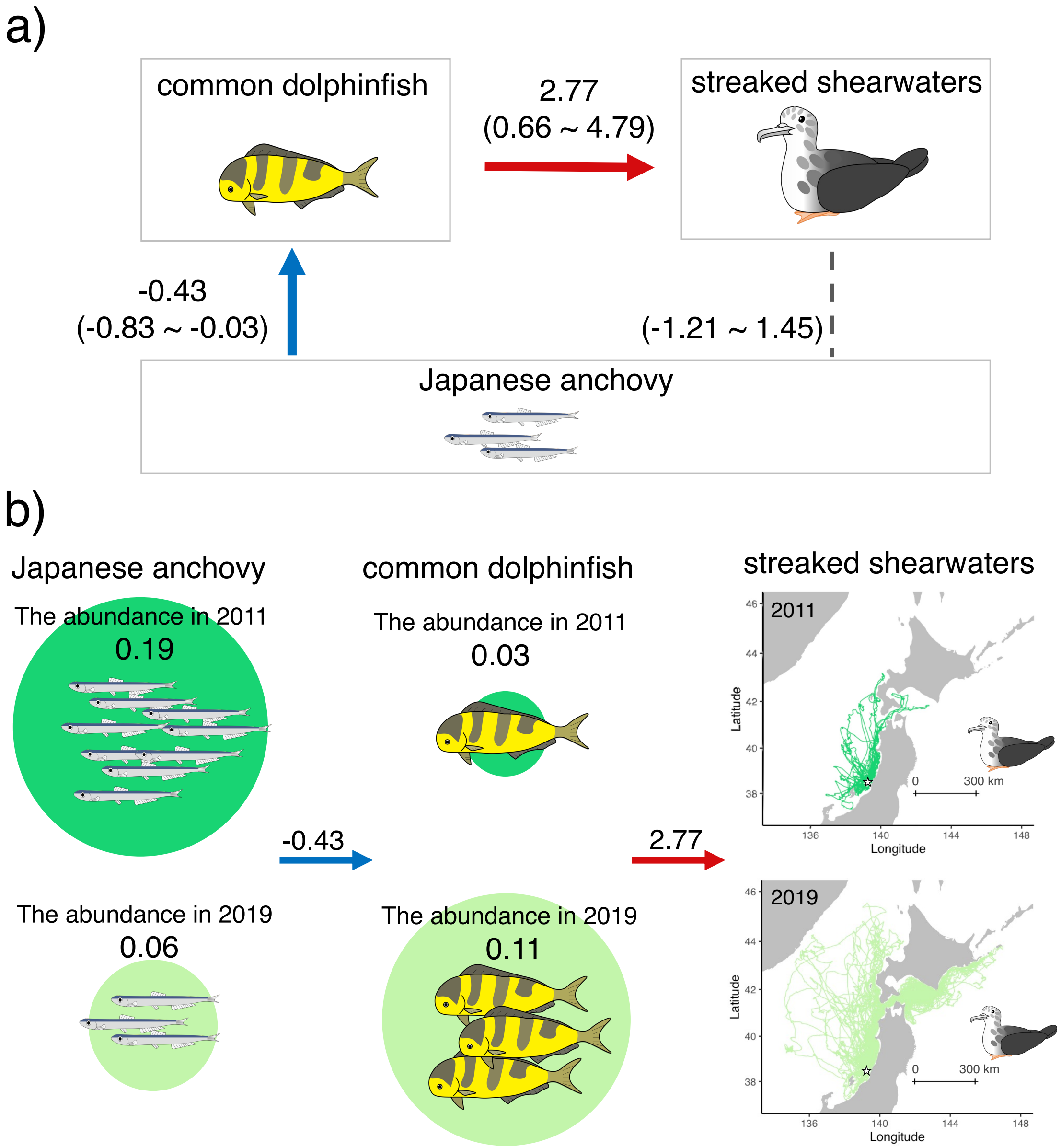


Figure 4.2: a) Relationships among the Japanese anchovy, common dolphinfish, and streaked shearwaters. The blue and red arrows indicate negative and positive relationships, respectively. The black dashed lines indicate no significant relationships. The numbers indicated close to the arrows and dashed lines are coefficients; mean (2.5–97.5%). b) The dark green GPS tracks (upper right panel) represent 2011 data, when the trip duration of streaked shearwaters in the SOJ was the shortest. The lighter green tracks (bottom right panel) represent 2019 data, when the trip duration of streaked shearwaters in the SOJ was the longest. The abundance was a relative value estimated from yearly fishery data for Japanese anchovy and common dolphinfish. The blue and red arrows indicate negative

and positive relationships, respectively. The numbers close to the arrows are the mean values of the coefficients. Foraging trajectories of streaked shearwaters in 2011 (blue lines) and 2019 (light blue lines) are shown on the right map. Foraging trips in which birds did not enter the Pacific Ocean were used in the analysis.

4.6. Appendix

Table S4.1: Sampling interval of GPS loggers, individual, and trip number.

Year	Logger	Sampling interval	Individual No.	Trip No.
2011	GiPSy-2	5 fix/1 min	23	96
2012	GiPSy-2	5 fix/1 min	40	120
2013	GiPSy-2	5 fix/1 min	10	54
	GiPSy-2	2 fix/10 sec	7	28
	GiPSy-4	1 fix/1 min	21	115
2014	GiPSy-2	5 fix/1 min	34	216
	GiPSy-4	1 fix/1 min	1	9
2015	GiPSy-2	5 fix/1 min	10	49
	GiPSy-4	1 fix/1 min	28	151
2016	GiPSy-2	5 fix/1 min	4	25
	GiPSy-4	1 fix/1 min	8	23
	GiPSy-5	1 fix/1 min	11	46
	Axy-Trek	1 fix/1 min	31	145

2017	GiPSy-4	1 fix/1 min	7	47
	GiPSy-5	1 fix/1 min	3	16
	Axy-Trek	1 fix/1 min	38	221
2018	Axy-Trek	1 fix/1 min	38	276
2019	Axy-Trek	1 fix/1 min	21	74
	PinPoint VHF	1 fix/5 min	11	202
2020	Axy-Trek	1 fix/1 min	14	61
	PinPoint VHF	1 fix/5 min	10	143
2021	Axy-Trek	1 fix/1 min	24	104
	Axy-Trek	1 fix/5 min	18	76

Table S4.2: Trip duration utilizing the SOJ and number of trips

Year	Trip duration of trips utilizing the SOJ (log)	Number of trips utilizing only the SOJ
2011	3.18	94
2012	3.41	107
2013	3.19	187
2014	3.24	218
2015	3.31	196
2016	3.48	232
2017	3.30	263
2018	3.13	265
2019	3.46	111
2020	3.35	184
2021	3.36	157

Table S4.3: Estimated value of Japanese anchovy abundance

Japanese anchovy	mean	2.50%	97.50%	R-hat
$a_{\mathrm{anchovy},2011}$	0.19	0.08	0.30	1.00
$a_{\mathrm{anchovy},2012}$	0.06	0.00	0.15	1.00
$a_{\mathrm{anchovy},2013}$	0.13	0.03	0.22	1.00
$a_{\mathrm{anchovy},2014}$	0.19	0.08	0.29	1.00
$a_{\mathrm{anchovy},2015}$	0.11	0.02	0.21	1.00
$a_{\mathrm{anchovy},2016}$	0.04	0.00	0.11	1.00
$a_{\mathrm{anchovy},2017}$	0.06	0.00	0.14	1.00
$a_{\mathrm{anchovy},2018}$	0.04	0.00	0.12	1.00
$a_{\mathrm{anchovy},2019}$	0.06	0.00	0.14	1.00
$a_{\mathrm{anchovy},2020}$	0.04	0.00	0.13	1.00
$a_{\mathrm{anchovy},2021}$	0.09	0.00	0.21	1.00
$B_{\mathrm{anchovy},Kyoto}$	482	308	697	1.00
$B_{\mathrm{anchovy},Toyama}$	394	239	616	1.00
$B_{\mathrm{anchovy},Fukui}$	51.32	29.69	81.43	1.00
$\sigma_{\mathrm{anchovy}}$	0.09	0.06	0.16	1.00

Table S4.4: Estimated value of common dolphinfish abundance

common dolphinfish	mean	2.50%	97.50%	R-hat
$a_{\mathrm{dolphinfish},2011}$	0.03	0.00	0.07	1.00
$a_{\mathrm{dolphinfish},2012}$	0.15	0.11	0.20	1.00
$a_{\mathrm{dolphinfish},2013}$	0.06	0.02	0.10	1.00
$a_{\mathrm{dolphinfish},2014}$	0.06	0.01	0.10	1.00
$a_{\mathrm{dolphinfish},2015}$	0.12	0.07	0.16	1.00
$a_{\mathrm{dolphinfish},2016}$	0.13	0.08	0.17	1.00
$a_{\mathrm{dolphinfish},2017}$	0.08	0.03	0.12	1.00
$a_{\mathrm{dolphinfish},2018}$	0.06	0.02	0.10	1.00
$a_{\mathrm{dolphinfish},2019}$	0.11	0.07	0.16	1.00
$a_{\mathrm{dolphinfish},2020}$	0.12	0.08	0.17	1.00
$a_{\mathrm{dolphinfish},2021}$	0.09	0.03	0.14	1.00
$B_{\mathrm{dolphinfish},Kyoto}$	784	603	1009	1.00
$B_{\mathrm{dolphinfish},Toyama}$	1460	1110	1897	1.00
$B_{\mathrm{dolphinfish},Fukui}$	1406	1078	1814	1.00
$B_{\mathrm{dolphinfish},Akita}$	33.66	25.30	44.52	1.00
$\sigma_{\mathrm{dolphinfish}}$	0.05	0.03	0.06	1.00

Table S4.5: Estimate value of hierarchical Bayesian modelling.

	mean	2.5%	97.5%	R-hat
d_1	0.13	0.09	0.17	1
d_2	-0.43	-0.83	-0.03	1
e_1	3.05	2.76	3.34	1
e_2	0.13	-1.21	1.45	1
e_3	2.77	0.66	4.79	1

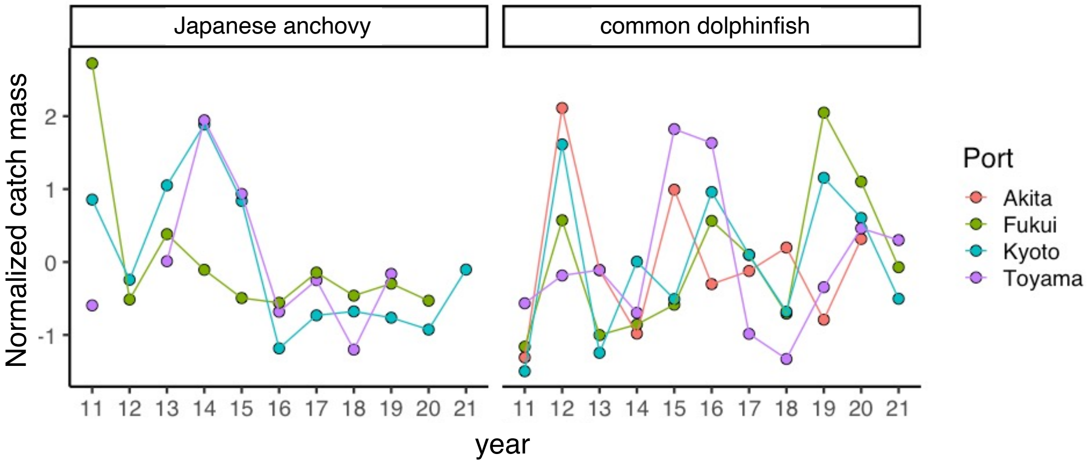


Figure S4.1: Annual fluctuations in catches (mass) by fixed-net method in four different areas in the SOJ. The numbers of year represent the last two digits of the year.

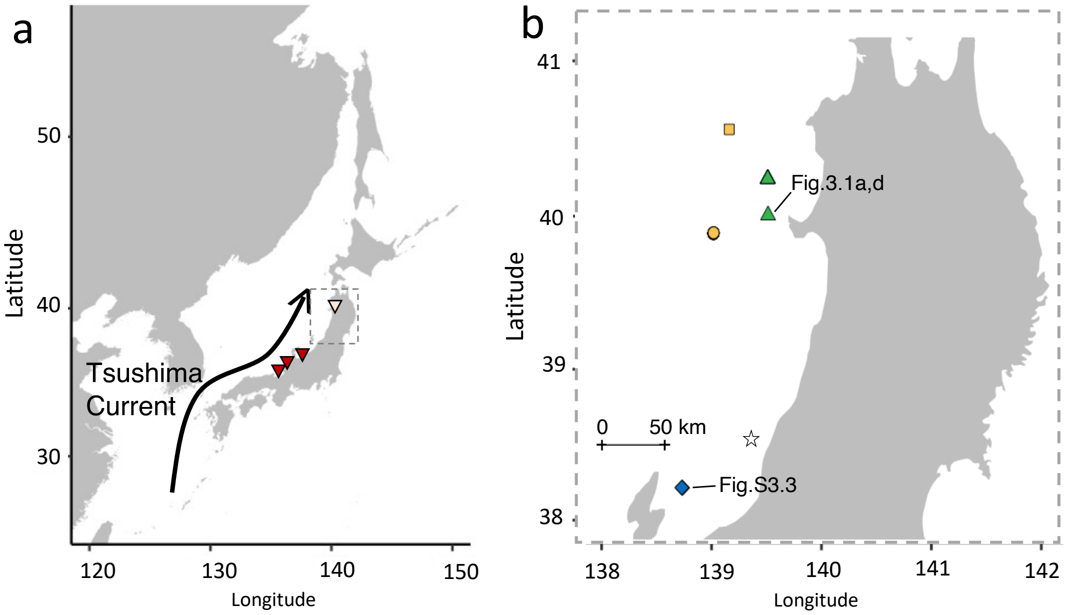


Figure S4.2: a) The map shows a portion of the Japanese archipelago. The gray areas indicate the land topography. The black line shows the flow of the Tsushima Warm Current. The fisheries data in prefectures, shown as red (Fukui, Toyama, and Kyoto) and light red (Akita) triangles were used to estimate the abundance of common dolphinfish in the SOJ. The data on fisheries in prefectures shown as red triangle were used to estimate the abundance of Japanese anchovy in the SOJ. b) Foraging points where large fish, supposedly common dolphinfish, were recorded by a video camera logger attached to streaked shearwaters (orange, green, and blue indicate the loggers attached in 2020, 2021, and 2022 respectively). Asterisks indicate colonies. The difference in point shapes (round, square, triangle, and rhombus) represent different individual shearwaters with data loggers attached. The gray areas indicate the land topography. The star indicates the location of the colony.

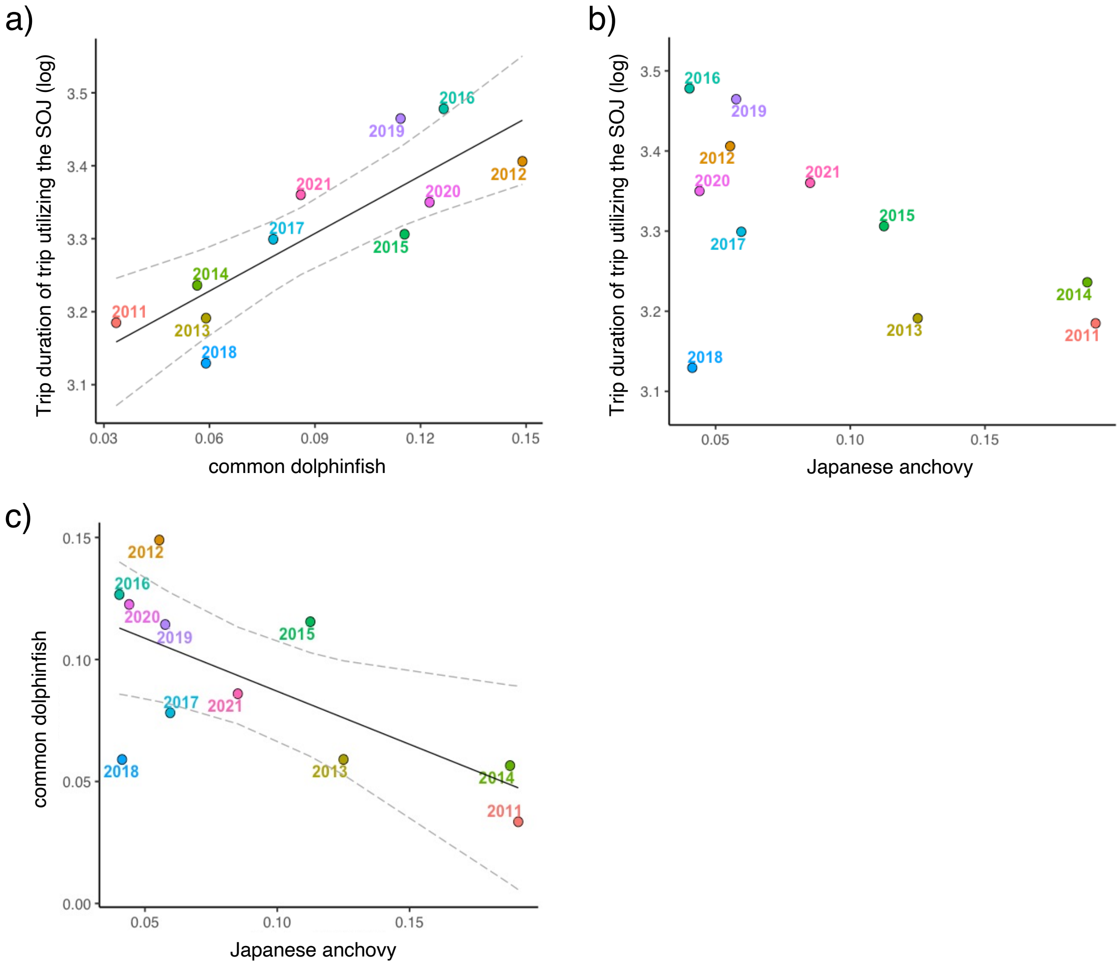


Figure S4.3: Relationships among Japanese anchovy, common dolphinfish, and streaked shearwaters. The upper and lower dashed gray lines indicate the 95% confidence intervals. a) There was a positive relationship between common dolphinfish and streaked shearwaters (solid line; intercept = 3.07, slope = 2.63). b) There was no relationship between Japanese anchovy and streaked shearwaters. c) There was a negative relationship between the Japanese anchovy and common dolphinfish (solid line; intercept = 0.13, slope = −0.43)

Chapter 5. Interannual linkages between oceanographic condition, seabird behavior, and reproduction from decadal bio-logging study

5.1 Introduction

Foraging animals face the major challenge of how to determine their foraging site and/or duration, according to the spatial distribution of their food and its availability in the surrounding environment. Foragers should distribute themselves by optimal choices of prey patches such that their net energy intake or fitness-related attributes is maximised, in scenarios with perfect knowledge of resource distribution and no travel costs between patches (Fretwell & Lucas, 1969; Pyke, 1984; Bergman et al., 2001). Such kind of foraging may be widespread in the animal kingdom, especially in long-lived birds and mammals that disperse over long distances with energy-saving adaptations (Hedenström, 2008; Avgar et al., 2014; Houston & Mcnamara 2014) and repeatedly sample their environment with superior memorisation (Bonadonna et al., 2001; Woo et al., 2008; Tessier & Bost, 2020). Thus, they could have evolved, to some degree, to cope and adapt with patchily distributed and annually changing habitats in the natural condition (Garthe et al., 2011; Robinson et al., 2012; Kuhn & Costa, 2014; Yamamoto et al., 2016b).

Another important factor for long-lived animals during the offspring-caring period is the trade-off between current and future reproduction, where optimal foraging is affected by present offspring demand or expectation of future reproduction (Erikstad et al., 1998; Rivalan et al., 2005; Hamel & Côté, 2008; Scharf et al., 2013). For example, supplementary feeding to parents increases their number of chicks in kestrels (Wiehn & Korpimäki, 1997) and reproductive effort reduces the survival of offspring in the subsequent year while not related to the maternal mortality in goats (Hamel et al., 2010), implying that they prioritise their own survival or future reproduction (Williams, 1966; Stearns, 1976). Long-lived foragers can resolve the trade-off by adjusting their foraging sites and/or behavior according to changes in the surrounding environment (Kitaysky et al., 2010; Staggenborg et al., 2017).

Consequently, the potential links and direction of causality between environments, foraging behavior of animals, and growth or survival of their offspring are expected to exist in the wild. For example, penguins breeding in different colonies show different foraging behaviors and chick growth (Tremblay & Cherel, 2003). In another example, increased food availability increases the body mass of female boars and kangaroos, resulting in a superior reproductive performance of those species (Gamelon et al., 2017; MacKay et al., 2018), demonstrating how environmental conditions can effects reproduction via animal behavior. In some cases, environmental factors, such as temperature and rainfall, influence offspring directly irrespective of parental behavior (Azzam et al., 1993; Woodroffe et al., 2017). It is of central interest to know not only such links exist, but also what degree parents are able to buffer against changes in foraging environments on reproduction (Elliott et al., 2014; Dehnhard et al., 2016; Kokubun et al., 2018; Schoen et al., 2018). In addition, the strength of effects in a hypothesized path may make it possible to discover causal processes hidden in complex ecological, behavioral, and reproductive patterns. The potential links emphasize the need for integrated studies that identify pathways between foraging behavior, environment, and offspring performance in wild animals.

Seabirds, one of the top predators in the marine ecosystem, change their distribution according to their surrounding environment (Pinaud & Weimerskirch, 2005; Grémillet & Boulinier, 2009; Kappes et al., 2010). Marine environments and resource availability influence seabirds' foraging behavior, such as their distribution, foraging duration, and distance from the colony (Pinaud et al., 2005; Garthe et al., 2011; Paiva et al., 2013; Serratosa et al., 2020). Regarding parental investment in chicks, some studies suggest that seabirds regulate the investment in their chick at a fixed level to maximise their survival (Ricklefs, 1987; Navarro & González-Solís, 2007), while others suggest that seabirds adjust their investment to chicks flexibly in response to demands of their chicks and their surrounding environment (Duriez et al., 2000; Weimerskirch et al., 2001). However, the elusive links and direction of causality between marine environments, foraging behavior of seabird parents, and growth of their offspring is still poorly understood, partly because prey resources are patchily distributed and often ephemeral which makes them difficult to measure.

Investigating interannual changes in environments, which is more clearly detectable than within-year changes, using decadal data provides insights of the behavioral and reproductive responses of seabird species, many of which breed once a year, to the changing environment. However, to the best of my knowledge, only a few studies have been conducted on decadal scale behavioral and reproductive responses of seabirds to marine environmental changes, especially due to the difficulties of collecting large datasets on seabird behavior (Weimerskirch et al., 2012; Thorne et al., 2015). Moreover, although previous studies provide data about the behavioral and reproductive responses, they have been conducted only on open seas with complex oceanographic systems (such as the Pacific and Southern Ocean), where seabirds move in all directions from the breeding colony. Consequently, these studies have demonstrated the behavioral and reproductive responses of seabirds to extreme and global environmental changes at the coarse scale, such as the Southern Annular Mode and its associated wind patterns (Weimerskirch et al., 2012) and El Niño and its associated SST changes (Thorne et al., 2015). Thus, information regarding the fine-scale linkages between oceanographic conditions, foraging behavior, and reproductive performance of seabirds is still lacking (note that marine environmental conditions such as SST may directly explain seabird population dynamics; Jenouvrier et al., 2018).

I focused on streaked shearwaters breeding in the SOJ, a semi-enclosed sea having one major current following south to north. Streaked shearwaters are an ideal species to examine the behavioral and reproductive responses of seabirds to marine environmental changes. The streaked shearwaters in the SOJ generally move in the north–south direction from the breeding colony for foraging and often decide either to stay in the SOJ or enter into the northwest PO through the narrow Tsugaru Strait, whose oceanographic features and prey species for the shearwaters differ from those of the SOJ (Kurasawa et al., 2012; Figure 5.1a). Such ecological system provides a unique opportunity to investigate binary choices of foraging habitats by seabirds and how they respond to marine environmental changes and chicks' demands.

I used behavioral and reproductive data of the streaked shearwaters obtained from 2011 to 2021 to test the following scenarios and six testable hypotheses (Figure S1; detailed in Methods) that explain the relationship between their surrounding environment, foraging behavior, and reproduction. I hypothesized that environmental parameters would affect foraging behavior (Matsumoto et al., 2017), i.e., the birds would be attracted to areas with high food availability, if streaked shearwaters are able to optimally select productive patches. I also hypothesized that the birds adjust their investment to chicks flexibly according to chick demand (Ogawa et al., 2015) and that the growth of chicks would affect their parental behavior—low chick growth increases food delivery rates, whereas foraging behavior may influence chick growth, i.e., low food delivery rates result in low chick growth, if the birds regulate the investment in their chick at a fixed level (Ricklefs, 1987; Navarro & González-Solís, 2007). I also hypothesized that the marine environment directly impacts offspring irrespective to their parental behavior (Jenouvrier et al., 2018).

5.2 Methods

5.2.1 Foraging movements of chick-rearing adults

For each foraging trip from 2011 to 2021 (Table S4.1), I calculated total flight distance as a proxy of flight costs for the birds, trip duration as a proxy of food delivery rate to their chick, and maximum distance from the colony as a proxy of how far birds fly away from the colony. The maximum distance from the colony was defined as the linear distance between the colony to the farthest GPS point from the colony. If the farthest GPS point from the colony was in the PO, the maximum distance from the colony was defined as the sum of the linear distance from the colony to the Tsugaru Strait (41°15′ N, 140°20′ E) and from the strait to a farthest GPS point from the straits. In addition, to examine their habitat-selection decisions, first, I select foraging trips with the maximum distance from the colony more than the linear distance between the colony and the Tsugaru Strait. Next, I classified trips according to whether the bird entered to PO (assigned as 1) or not (assigned as 0) as described in chapter 4.2.2.

In the later analyses (see later subsection 5.2.4. *Statistical analysis*), I used yearly averages of total flight distance, trip duration, and maximum distance from the colony, as well as yearly probabilities of entering the PO. In obtaining these yearly averages, it is desirable to remove the effect of individual variation rather than taking a simple yearly average because the trip data includes trips of the same individual, either in the same year and/or across years. To this end, I applied GLMM for each variable, with them as response variables, year as a categorical explanatory variable, and individual ID as a random effect, and then, the mean value of each variable for each year were estimated (Table S5.1). The total flight distance, trip duration, and maximum distance from the colony were log-transformed, and a normal distribution was used as the probability distribution. The probability of entering the PO was obtained by fitting a logistic regression with a binomial distribution, taking the response variable as whether or not the flight was to PO (1 or 0). I utilized the glmmTMB function of glmmTMB package (Brooks et al., 2022).

From the GPS data, the distribution of streaked shearwaters was calculated by kernel density analysis using the “kernelUD” function in the adehabitatHR package (Calenge, 2019; Figure 5.1a).

5.2.2 Chick growth rate

To monitor the reproduction of streaked shearwaters in the colony, the chicks were weighed annually from 2011 to 2021. The parents of these chicks were not included in any experiments, including the attachment of the GPS loggers. From a few days after hatching early to mid-August to fledgling, I measured the body mass of each chick every 5 days in 5 g units using a spring scale. To estimate their age, I measured their wing length in 1-mm units using a ruler. I estimated age and hatching date using wing lengths measured at least five times during September (Shirai, 2016). Food provision by their parents was not disturbed because I conducted these measurements during the daytime when their parents were away on foraging trips.

The chicks of streaked shearwaters hatch in mid-August, gain body mass until mid-October (when the parents migrate south), and fledge in the end of October to early November (Oka et al., 2002; Yoda et al., 2017). Because the body mass of chick reflects the meal mass brought by parents (Ogawa et al., 2015), changes in body mass (growth rate) of the chicks was calculated. I approximated the growth curve as a cubic curve (Weimerskirch et al., 2000) using the nonlinear least-squares method with the "nls" function in R by taking the body mass of each individual that survived until October 15th (Figure S5.2). The chick growth rate was calculated as the tangent slope at 50% of the maximum value of the approximate growth curve (Shirai, 2016). The mean values for each year were calculated as yearly chick growth rate. Chick survival rate was not used since it is often irrelevant for marine environment and parental foraging behavior due to predation by feral cats (Shiozaki et al., 2014).

5.2.3 Environmental parameters

Although a wide variety of seabird species utilizes marine-derived food resources, there are no environmental indicators that are directly related to the quantity or quality of their prey resources. The mean value of SST and coefficient of variation of SST are often used as a proxy of biomass productivity (Parsons et al., 2008; Einoder, 2009; Chavez et al., 2011). Especially, coefficient of variation of SST is related to major hydrographic features which enhance biomass productivity such as upwelling, front, and current mixing (Becker & Beissinger 2003; Bost et al., 2009; Serratosa et al., 2020). Since streaked shearwaters breeding on Awashima Island tend to fly to the PO in years when the mean SST around the colony is high (Matsumoto et al., 2017; using data from 2011 to 2013), I used the mean SST and its coefficient of variation as indirect proxies of food availability. I downloaded daily SST values from 20 August to the end of September corresponding to the chick-rearing period of streaked shearwaters from 2011 to 2021 (Figure 5.1; 0.05° resolution; downloaded from NOAA Coral Reef Watch). Using these data, I calculated the mean SST and its variability during each sampling day (coefficient of variation) in the SOJ for the 25% kernel ranges used by streaked shearwaters. I also calculated them in the PO region, defined as the east region of the line connecting the two points on the east of the Tsugaru Strait, for 75% kernel ranges used by the birds.

5.2.4 Statistical analysis

To investigate the relationships between SST, foraging behavior, and chick growth rate, I conducted path analysis using the “cfa” function in the lavaan package (Rosseel et al., 2022). Path analysis is an extension of multiple regression analysis for examining relationships among variables through a set of explicit assumptions about causal relationships. I used path analysis to examine the relationships between SST, foraging behavior, and chick growth, using a data set with sample size of 11 obtained from 2011 to 2021. I tested the following six models (Figure S5.1). A) the environment has a direct effects on parental foraging behavior and chick growth, and the former influences chick growth; B) the environment influences parental foraging behavior and chick growth, the latter of which influences parental behavior; C) the environment influences parental foraging behavior and chick growth, with no relationship between parent and offspring; D) the environment influences parental foraging behavior that affects chick growth; E) the environment and chick growth influence parental behavior; and F) the environment influences parental behavior. In summary, models A–F correspond to the hypothesis related to optimal habitat selection theories that environmental parameters would affect foraging behavior. Models A, B, D, and E correspond to the hypothesis related to fixed (A and D) or flexible (B and E) investment theories that chick growth would influence parental behavior (B and E), and vice versa (A and D). Models A, B, and C correspond to the hypothesis that the marine environment would affect offspring directly irrelevant of parental behavior. Model F corresponds to the alternative hypothesis that neither environment nor foraging behavior do not influence chicks. By using data of SST (mean of SST in the SOJ, coefficient of variation in the SOJ, mean of SST in the PO, and coefficient of variation in the PO), foraging behavior (log-transformed total flight distance, log-transformed trip duration, log-transformed maximum distance from the colony, or probability of entering the PO), and chick growth, I constructed 216 models in all possible combinations where all values were normalized (Table S5.2 and Table S5.3). The goodness-of-fit of each model was evaluated using the goodness-of-fit index (GFI) and root mean square error of approximation index (RMSEA). GFI > 0.9 and RMSEA < 0.05 indicated a good model fit to the data; the best model was assessed based on AIC.

To confirm the relationship between the coefficient of variation of SST, the probability of entering the PO, and chick growth rate, which was chosen as the best model in the path analysis, I constructed a GLM, using the glm function in the lm4 package (Bates et al., 2022), where the coefficient of variation of SST and chick growth rate were the explanatory variables, and the probability of entering the PO was a response variable.

5.3 Results

I obtained data for 2183 foraging trips by 414 chick-rearing streaked shearwaters (265 individuals) from 2011 to 2021 (Figure 5.1) and calculated yearly values of trip parameters (Table 5.1 and Table S5.1). I measured the body mass of 190 chicks and calculated the chick growth rate of each individual and the yearly mean of the chick growth rate (Figure S5.2 and Table S5.1).

The best model included the probability of entering the PO as a response variable and coefficient of variations of SST in the SOJ, coefficient of variations of PO, and chick growth rate as explanatory variables was selected as the best model, yielding a reasonably good fit of the data (GFI = 1.00, RMSEA = 0, AIC = –12.44, Figure 5.2, Table 5.2). The parameters used in the best model are shown in Table 5.1. In the best model, the coefficient of variation of SST in the PO ($P = 0.00$, estimate = 1.09) had positive effects on the probability of entering the PO. The coefficient of variation of SST in the SOJ ($P = 0.01$, estimate = –0.53) and chick growth rate ($P = 0.00$, estimate = –0.12) had negative effects on the probability of entering the PO (Table 5.3).

Additional analyses using GLM showed that the coefficient of variation of SST in the PO had a positive relationship with the probability of entering the PO (P = 0.00). The coefficient of variation of SST in the SOJ had marginally negative effect (P = 0.07) on the probability of entering the PO while the chick growth rate had a negative effect (P = 0.03; Table 5.4).

5.4 Discussion

Using decadal-scale bio-logging data of seabirds, I demonstrated the clear behavioral responses of wild seabirds to marine environmental changes, which have been previously shown only at coarse scales (Weimerskirch et al., 2012; Thorne et al., 2015). By employing long-term bio-logging approaches to wild shearwaters foraging in distinct ocean areas with different oceanographic features, I found that a smaller variability in the SST of the SOJ tended to drive streaked shearwaters to forage in the PO, whereas a larger variability in the SST of the PO and low chick growth rate attracted seabirds toward the PO. Environmental variability related to major hydrographic features rather than the mean value might affect the behavior of seabirds in a similar way to how the SST variability influences population dynamics (Pardo et al., 2017). My results suggest that environmental variability in space might be important for animal behavior in addition to the environmental mean value as described in studies of population dynamics (García-Carreras & Reuman, 2013; Lawson et al., 2015).

In the PO, a larger variability in SST attracted streaked shearwaters to the area. Variability in SST indicates sea surface circulation; a smaller variability in SST would indicate low marine productivity and poor food availability for seabirds (Abraham & Sydeman, 2004). The larger variability in SST in the PO may indicate that this is an area of high marine productivity due to the mixing of ocean currents, such as the Oyashio–Kuroshio transition zone (Wang et al., 2010; Checkley et al., 2017; Qiu, 2019). On the other hand, a smaller variability in SST in the SOJ tended to drive streaked shearwaters to the PO. The availability or the lack of prey resources is known to attract or repel predators, affecting their distribution (Nathan et al., 2008). Likewise, the distribution of marine animals (including seabirds) may also be determined by different water masses (i.e., food resources) attracting or repelling them (Hyrenbach et al., 2002).

One other factor that could account for the probability of entering the PO in addition to marine productivity is chick growth rates, i.e., a proxy for meal mass brought to the chick, with smaller growth rates leading to a high probability of entering the PO. Some of seabird species adjust their foraging behavior according to their chick's requirements (Bertram et al., 1996; Weimerskirch et al., 1997b; Hamer et al., 1999; Ito et al., 2010; Botha & Pistorius 2018). Likewise, streaked shearwaters extend their next foraging trip after their chick is well fed (Ogawa et al., 2015). Streaked shearwaters might travel to the PO and obtain high energy prey such as pacific saury in the PO when the chick is not feed (Kurasawa et al., 2012; Mastumoto et al., 2012; Ochi et al., 2016). Foraging in areas in the PO might have an important role in chick growth of shearwaters, as suggested by a long duration trip which provides high energy stomach oil to chicks of Procellariiformes (Warham et al., 1976; Ochi et al., 2016). Seabirds might decide on their foraging site flexibly according to demands from chicks and shape their distribution.

The path analysis also indicated the strength of the associations between food availability of different areas, foraging behavior, and the chick requirements. The effect of the variability of SST in the PO on whether the birds entering the PO was approximately twice as large as that of the effect of the variability of SST in the SOJ. Moreover, the probability was negatively influenced by the chick growth rates, but the effect was small compared to the environmental variabilities. Thus, the birds might prioritize the food abundance in the PO over that in the SOJ and chick demands, implying that they do not enter the PO when the prey abundance of the PO is low, even if either chick growth or food availability in the SOJ are low. The relatively small effect of the chick requirements on the foraging behavior compared to food availability might be reasonable for long-lived birds that are supposed to prioritize future over current reproduction (Sæther et al., 1993; Harding et al., 2009; Booth & McQuaid, 2013; Kidawa et al., 2017). Likewise, areas of particularly high prey availability (Waugh et al., 1999; Weimerskirch, 2007; Bost et al., 2009) or with different oceanographic properties from those around the colony (Hyrenbach et al., 2002) may have more significant effects on the overall system of seabird foraging decisions than food availability around the colony or the chick requirements do.

The interannual and population-scale results of this study supported the general theory that predators change their foraging site to adapt to heterogeneous and unpredictable food availability (Fretwell & Lucas, 1969; Sih, 2005; Fauchald, 2009). Although it is difficult to observe directly, in a complex and dynamically changing environment, predators might freely distribute themselves to overlap with their prey, in the same locations (Briggs & Hoopes, 2004). This flexible foraging movement in long-lived predators, including seabirds, might be related to a trade-off between self-maintenance for future reproduction and feeding chicks (Granadeiro et al., 1998).

My results imply that foraging movement of streaked shearwaters could be used as an indicator of marine productivity as has been suggested in other seabirds (Parsons et al., 2008; Einoder, 2009). In the years when streaked shearwaters tend to forage at PO, marine productivity i.e., food availability for streaked shearwaters, may be low in the SOJ and/or high in the PO. This study could provide a guide for marine management that high coefficient of variation areas might be high productivity areas that is crucial for the marine ecosystem (Serratosa et al., 2020). Long-term monitoring of seabird behavioral and reproductive factors would allow us to detect crucial marine area for marine ecosystem and assess marine productivity (Einoder, 2009).

Overall, my study system demonstrated clear behavioral responses of wild seabirds to marine environmental changes using decadal data; spatial ocean dynamics would attract or repel predators, which could be also affected by offspring demands. I encourage future work to apply the path analyses used in this study to other marine animals with decadal data sets to untangle the complex behavioral and ecological effects. Moreover, this study opens interesting research questions regarding how individuals with different attributes (e.g., age, sex, and physiological states) could be optimal foragers that are able to perceive high food availability areas and choose optimal feeding sites in response to environmental changes and chick requests. Such work could provide integrative insights of foraging and reproductive behavior of animals in the dynamically changing environments.

5. 5 Tables and figures

Table 5.1: Yearly data of the mean of SST in the SOJ, mean of SST in the PO, coefficient of variation of SST in the SOJ, coefficient of variation of SST in the PO, and probability of entering the PO. The path models include the five parameters found in the most accurate model. SST, sea surface temperature; SOJ, Sea of Japan; PO, Pacific Ocean

	coefficient of variation of SST		probability of entering the PO	chick growth rate (g/day)
year	SOJ	PO		
2011	1.23	0.89	0.22	17.15
2012	0.90	0.86	0.50	15.16
2013	1.05	0.97	0.65	15.83
2014	0.90	0.87	0.51	16.56
2015	1.04	0.46	0.094	15.26
2016	1.31	0.47	0.086	14.65
2017	1.12	0.83	0.54	14.24
2018	1.15	0.50	0.29	14.74
2019	1.06	0.92	0.85	14.74
2020	1.37	0.98	0.68	14.38
2021	0.89	0.77	0.62	16.10

Table 5.2: Goodness-of-fit (GFI), root mean square error of approximation index (RMSEA), and AIC of the top three models of the best model set with the smallest AIC. Arrows represent the relationships between variables. sea surface temperature; SST, the Sea of Japan; SOJ, Pacific Ocean; PO

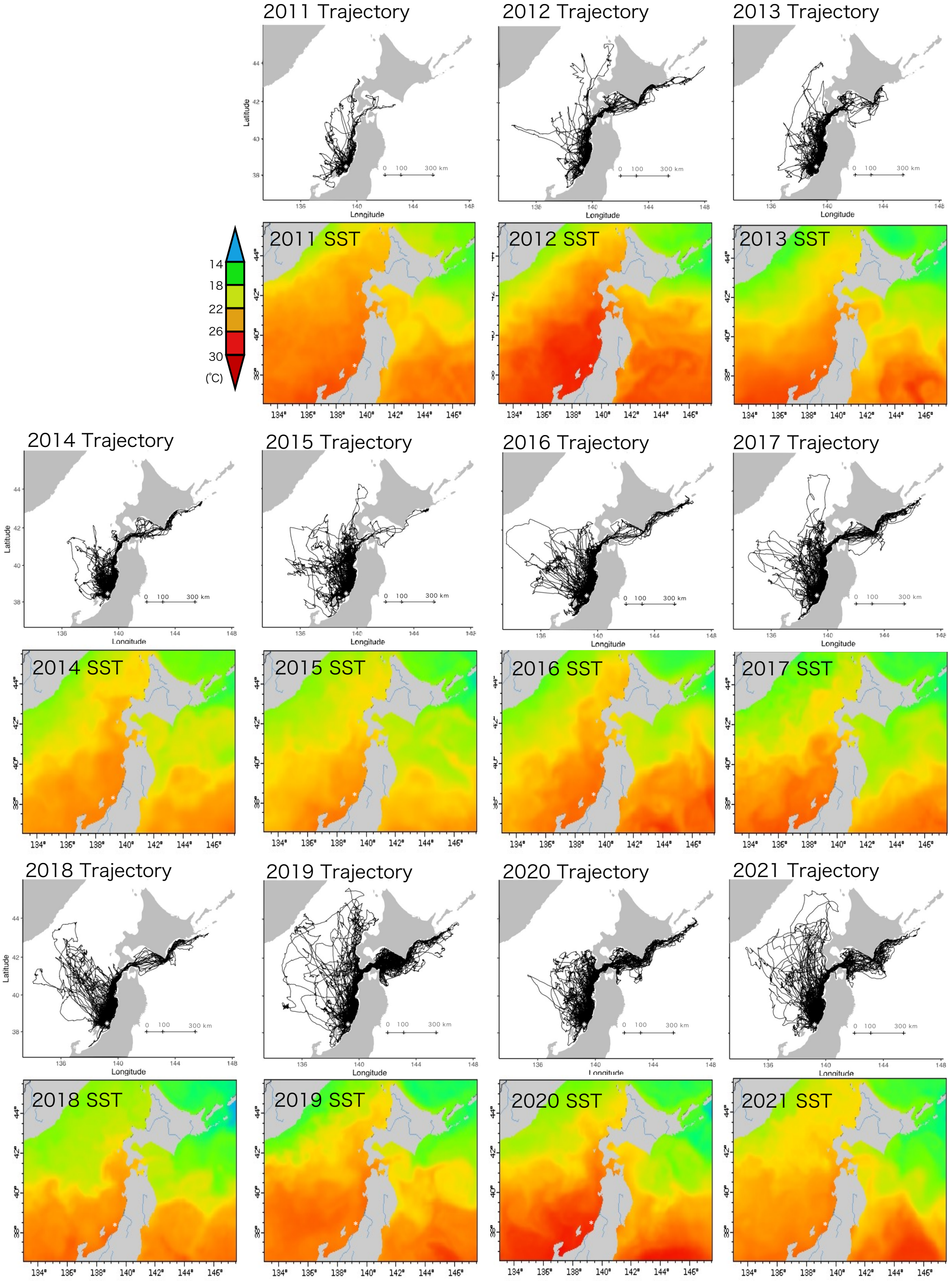
Parameter Estimate	GFI	RMSEA	AIC
probability of entering the PO ← coefficient of variation of SST in the SOJ probability of entering the PO ← coefficient of variation of SST in the PO probability of entering the PO ← chick growth rate	1.00	0	–12.44
probability of entering the PO ← mean of SST in the SOJ probability of entering the PO ← coefficient of variation of SST in the SOJ probability of entering the PO ← coefficient of variation of SST in the PO probability of entering the PO ← chick growth rate	1.00	0	–11.83
probability of entering the PO ← mean of SST in the PO probability of entering the PO ← coefficient of variation of SST in the SOJ probability of entering the PO ← coefficient of variation of SST in the PO probability of entering the PO ← chick growth rate	1.00	0	–11.53

Table 5.3: Statistical estimates of the best model in the path analysis. Arrows represent the relationships between variables. SST, sea surface temperature; SOJ, Sea of Japan; PO, Pacific Ocean; S.E., standard error

Parameter Estimate	Estimate	S.E.	z value	*P* value
probability of entering the PO ← coefficient of variation of SST (SOJ)	–0.53	0.20	–2.67	0.008
probability of entering the PO ← coefficient of variation of SST (PO)	1.09	0.16	6.99	0.000
probability of entering the PO ← chick growth rate	–0.12	0.035	–3.50	0.000
error variable [probability of entering the PO]	0.0090	0.0040	2.35	0.019

Table 5.4: Statistical estimates of GLM. SST, sea surface temperature; SOJ, Sea of Japan; PO, Pacific Ocean; S.E., standard error; *P*, P-value

	Estimate	S. E.	t value	*P*
Intercept	2.10	0.81	2.58	0.036
coefficient of variation of SST (SOJ)	–0.53	0.25	–2.13	0.071
coefficient of variation of SST (PO)	1.09	0.20	5.58	0.00084
chick growth rate	–0.12	0.044	–2.79	0.027



2011 Trajectory

2012 Trajectory

2013 Trajectory

2011 SST

2012 SST

2013 SST

2014 Trajectory

2015 Trajectory

2016 Trajectory

2017 Trajectory

2014 SST

2015 SST

2016 SST

2017 SST

2018 Trajectory

2019 Trajectory

2020 Trajectory

2021 Trajectory

2018 SST

2019 SST

2020 SST

2021 SST

Figure 5.1: Trajectory of streaked shearwaters and sea surface temperatures. Trajectory of streaked shearwaters between August and September of each year from 2011 to 2020 (black lines). Sea surface temperatures on September 1st of each year from 2011 to 2021 are shown in this figure. The grey areas show the land topography. The white star indicates the location of the study site.

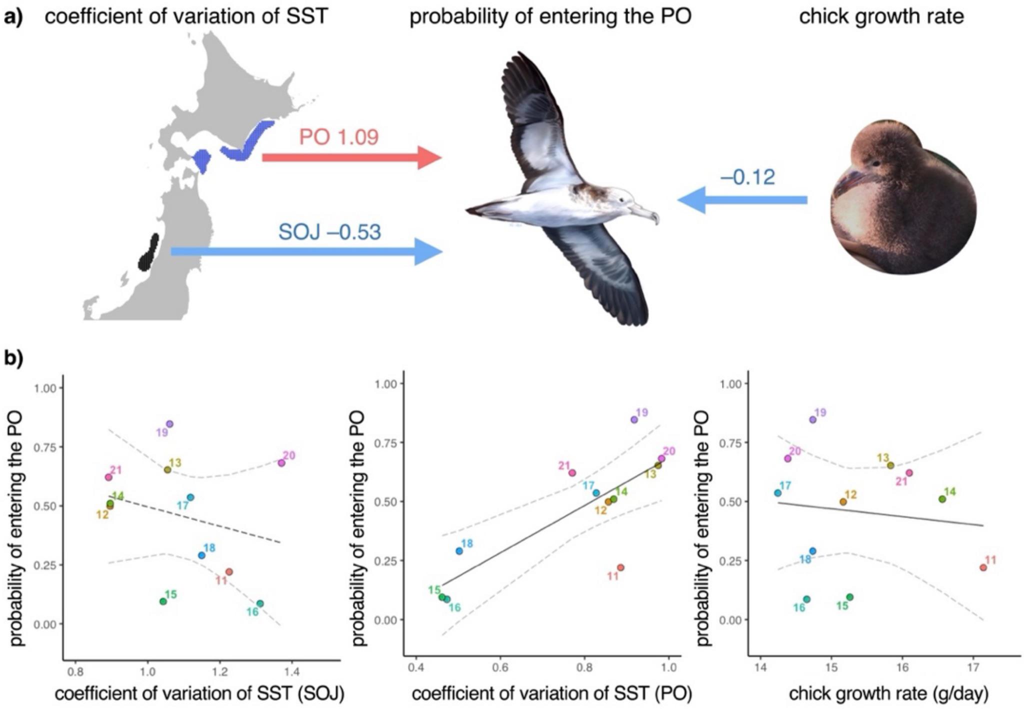


Figure 5.2: a) Statistical estimate of the path analysis model, including coefficient of variation of SST in the Sea of Japan (SOJ), coefficient of variation of the SST in the Pacific Ocean (PO), probability of entering the PO. The mean and coefficient of variation of SST were calculated for the black area of the SOJ, corresponding to 25% utilization distributions of the birds, and dark blue area of the PO, corresponding to 75% utilization distributions of the birds on the left map. Red and blue arrows indicate positive and negative relationships, respectively. b) Relationship between probability of entering the PO and coefficient of variation of SST in the SOJ, coefficient of variation of the SST in the PO, and chick growth rate. The left panel shows the negative relationship between coefficient of variation of SST in SOJ and the probability of entering the PO (dashed black line; intercept = 0.91, slope = –0.41). The middle panel shows the positive relationship between coefficient of variation of SST in PO and the probability of entering the PO (solid black line; intercept = –0.32, slope = 1.00). The right panel shows the negative relationship between chick growth rate and the probability of entering the PO (solid black line; intercept = –0.034, slope = 0.97). Upper and lower dashed grey lines in the figures are 95% confidence intervals. The numbers written near the dots represent the last two digits of the year.

5.6 Appendix

5.6.1 Appendix methods

To confirm the relationship between yearly behavioural and reproductive parameters and the sample number, we constructed a linear model using the “lm” function in R.

5.6.2 Appendix results

We confirmed that there was no relationship between the foraging Chase behavior and the number of foraging trips by constructing a linear model (log-transformed total flight distance; $P = 0.99$, log-transformed trip duration; $P = 0.38$, log-transformed maximum distance from the colony; $P = 0.91$, probability of entering the Pacific Ocean; $P = 0.61$), nor a relationship between the chick growth rate and sample size of chick ($P = 0.36$).

When a path from the mean of SST in the SOJ to the probability of entering the PO was added to the best model, it was selected as the second-best model, but there was no significant relationship between the mean of SST in the SOJ and the probability of entering the PO ($P = 0.29$; Table S5.4). When a path from the mean of SST in the PO to the probability of entering the PO was added to the best model, it was selected as the third-best model, but there was no significant relationship between the mean of SST in the PO and the probability of entering the PO ($P = 0.22$; Table S5.4).

Table S5.1: Mean value of SST in the SOJ and in PO, the logarithmic transformed total flight distance, logarithmic transformed trip duration, and logarithmic transformed maximum distance from the colony from 2011 to 2021.

Year	Mean of SST in SOJ (°C)	Mean of SST in PO (°C)	Total flight distance	Trip duration	Maximum distance from the colony
2011	25.25	19.68	5.43	3.2	4.16
2012	27.59	21.46	5.87	3.6	4.45
2013	25.88	20.11	5.77	3.28	4.44
2014	24.86	19.46	5.66	3.29	4.34
2015	23.93	19.23	5.88	3.34	4.54
2016	25.64	20.23	5.93	3.51	4.67
2017	24.88	18.14	5.94	3.39	4.70
2018	24.85	18.56	5.6	3.19	4.34
2019	25.77	19.55	6.39	3.88	5.18
2020	27.07	20.73	5.78	3.44	4.58
2021	24.99	19.06	6.07	3.57	4.94

Table S5.2: Goodness-of-fit (GFI), Adjusted Goodness-of-fit (AGFI), root mean square error of approximation index (RMSEA), and AIC of each model of path analyses. The models are described in Figure S1. The SST parameters shown in grey were added to the model. sea surface temperature; SST, the Sea of Japan; SOJ, the Pacific Ocean; PO, coefficient of variation; CV, log-transformed trip duration; TD, probability of entering the Pacific Ocean; P, log-transformed total flight distance; T, log-transformed maximum distance from the colony; M

SOJ (SST)		PO (SST)							
mean	CV	mean	CV	behavior	GFI	AGFI	RMSEA	AIC	model
	■		■	P	1.00	1.00	0.00	-12.44	E
	■	■	■	P	1.00	1.00	0.00	-11.83	E
■	■		■	P	1.00	1.00	0.00	-11.53	E
■	■	■	■	P	1.00	1.00	0.00	-9.83	E
■			■	P	1.00	1.00	0.00	-7.98	E
■	■	■	■	P	1.00	1.00	0.00	-6.63	F
■		■	■	P	1.00	1.00	0.00	-6.32	E
■		■	■	P	1.00	1.00	0.00	-6.29	F
	■		■	P	1.00	1.00	0.00	-6.20	F
■			■	P	1.00	1.00	0.00	-5.21	F
	■	■	■	P	1.00	1.00	0.00	-4.82	F
■	■		■	P	1.00	1.00	0.00	-4.30	F
	■	■		TD	1.00	1.00	0.00	-1.98	E

	■		■	TD	1.00	1.00	0.00	-1.42	E
■	■	■		P	1.00	1.00	0.00	-0.96	F
■		■		TD	1.00	1.00	0.00	-0.74	F
■			■	TD	1.00	1.00	0.00	-0.65	F
	■	■	■	TD	1.00	1.00	0.00	-0.58	E
	■	■		TD	1.00	1.00	0.00	-0.30	F
■	■		■	TD	1.00	1.00	0.00	-0.14	E
■	■	■		TD	1.00	1.00	0.00	-0.13	E
■		■		P	1.00	1.00	0.00	-0.08	F
■			■	TD	1.00	1.00	0.00	0.03	E
■		■		TD	1.00	1.00	0.00	0.21	E
■	■	■		TD	1.00	1.00	0.00	0.38	F
■	■		■	TD	1.00	1.00	0.00	0.45	F
	■		■	TD	1.00	1.00	0.00	0.45	F
■	■	■		P	1.00	1.00	0.00	0.91	E
■		■		P	1.00	1.00	0.00	1.12	E
■		■	■	TD	1.00	1.00	0.00	1.23	F
■	■	■	■	TD	1.00	1.00	0.00	1.33	E
	■		■	F	1.00	1.00	0.00	1.57	E
	■	■	■	TD	1.00	1.00	0.00	1.63	F

▨		▨	▨	TD	1.00	1.00	0.00	1.73	E
	▨	▨		F	1.00	1.00	0.00	2.02	E
▨	▨	▨	▨	TD	1.00	1.00	0.00	2.20	F
▨	▨		▨	F	1.00	1.00	0.00	3.27	E
	▨	▨	▨	F	1.00	1.00	0.00	3.57	E
▨	▨	▨		F	1.00	1.00	0.00	3.97	E
▨	▨	▨	▨	F	1.00	1.00	0.00	4.28	E
▨			▨	F	1.00	1.00	0.00	4.39	E
	▨	▨		P	1.00	1.00	0.00	4.75	F
▨		▨		F	1.00	1.00	0.00	5.19	E
	▨		▨	F	1.00	1.00	0.00	5.35	F
	▨	▨		F	1.00	1.00	0.00	5.36	F
▨		▨		F	1.00	1.00	0.00	5.45	F
▨		▨	▨	F	1.00	1.00	0.00	5.85	E
▨			▨	F	1.00	1.00	0.00	5.86	F
	▨	▨		P	1.00	1.00	0.00	5.92	E
	▨		▨	M	1.00	1.00	0.00	6.65	E
▨	▨	▨		F	1.00	1.00	0.00	6.66	F
	▨	▨		M	1.00	1.00	0.00	6.91	E
▨	▨		▨	F	1.00	1.00	0.00	7.15	F

▨			▨	M	1.00	1.00	0.00	7.20	E
	▨	▨	▨	F	1.00	1.00	0.00	7.35	F
▨		▨	▨	F	1.00	1.00	0.00	7.41	F
▨	▨		▨	M	1.00	1.00	0.00	7.84	E
▨		▨		M	1.00	1.00	0.00	7.95	F
	▨	▨	▨	M	1.00	1.00	0.00	8.25	E
▨		▨		M	1.00	1.00	0.00	8.25	E
▨	▨	▨	▨	F	1.00	1.00	0.00	8.47	F
	▨	▨		M	1.00	1.00	0.00	8.56	F
	▨		▨	M	1.00	1.00	0.00	8.74	F
▨			▨	M	1.00	1.00	0.00	8.88	F
▨	▨	▨		M	1.00	1.00	0.00	8.90	E
▨		▨	▨	M	1.00	1.00	0.00	9.10	E
▨	▨	▨	▨	M	1.00	1.00	0.00	9.66	E
▨	▨	▨		M	1.00	1.00	0.00	9.69	F
▨		▨	▨	M	1.00	1.00	0.00	9.94	F
	▨	▨	▨	M	1.00	1.00	0.00	10.47	F
▨	▨		▨	M	1.00	1.00	0.00	10.73	F
▨	▨	▨	▨	M	1.00	1.00	0.00	11.63	F
▨	▨	▨	▨	P	1.00	1.00	0.00	19.01	B

▨	▨	▨	▨	P	1.00	1.00	0.00	19.01	C
▨	▨	▨	▨	P	1.00	1.00	0.00	19.01	A
	▨		▨	P	1.00	1.00	0.00	20.22	A
	▨		▨	P	1.00	1.00	0.00	20.22	B
	▨		▨	P	1.00	1.00	0.00	20.22	C
▨	▨		▨	P	1.00	1.00	0.00	21.29	A
▨	▨		▨	P	1.00	1.00	0.00	21.29	B
▨	▨		▨	P	1.00	1.00	0.00	21.29	C
▨		▨	▨	P	1.00	1.00	0.00	21.38	A
▨		▨	▨	P	1.00	1.00	0.00	21.38	B
▨		▨	▨	P	1.00	1.00	0.00	21.38	C
	▨	▨	▨	P	1.00	1.00	0.00	22.83	A
	▨	▨	▨	P	1.00	1.00	0.00	22.83	B
	▨	▨	▨	P	1.00	1.00	0.00	22.83	C
▨			▨	P	1.00	1.00	0.00	23.85	A
▨			▨	P	1.00	1.00	0.00	23.85	C
▨			▨	P	1.00	1.00	0.00	23.85	B
▨	▨	▨	▨	P	0.90	0.49	0.50	26.11	D
▨		▨	▨	P	0.87	0.36	0.49	26.45	D
	▨		▨	P	0.83	0.14	0.61	26.53	D

■			■	P	0.83	0.16	0.51	27.52	D
	■	■	■	P	0.84	0.19	0.49	27.91	D
■	■		■	P	0.81	0.06	0.55	28.44	D
■		■	■	TD	1.00	1.00	0.00	29.43	B
■		■	■	TD	1.00	1.00	0.00	29.43	A
■		■	■	TD	1.00	1.00	0.00	29.43	C
■	■	■	■	TD	1.00	1.00	0.00	30.17	A
■	■	■	■	TD	1.00	1.00	0.00	30.17	B
■	■	■	■	TD	1.00	1.00	0.00	30.17	C
■		■		TD	0.84	0.20	0.13	30.55	D
■			■	TD	0.82	0.10	0.19	30.64	D
	■	■		TD	0.77	-0.13	0.29	30.99	D
	■	■		TD	1.00	1.00	0.00	31.13	B
	■	■		TD	1.00	1.00	0.00	31.13	A
	■	■		TD	1.00	1.00	0.00	31.13	C
	■		■	TD	1.00	1.00	0.00	31.23	A
	■		■	TD	1.00	1.00	0.00	31.23	B
	■		■	TD	1.00	1.00	0.00	31.23	C
■	■	■		TD	0.73	-0.37	0.27	31.67	D
■	■		■	TD	0.74	-0.31	0.25	31.74	D

	▨		▨	TD	0.75	-0.26	0.34	31.74	D
▨	▨	▨		P	0.84	0.19	0.21	31.77	D
▨			▨	TD	1.00	1.00	0.00	31.86	B
▨			▨	TD	1.00	1.00	0.00	31.86	A
▨			▨	TD	1.00	1.00	0.00	31.86	C
▨		▨		TD	1.00	1.00	0.00	32.18	B
▨		▨		TD	1.00	1.00	0.00	32.18	C
▨		▨		TD	1.00	1.00	0.00	32.18	A
▨	▨	▨		TD	1.00	1.00	0.00	32.21	B
▨	▨	▨		TD	1.00	1.00	0.00	32.21	A
▨	▨	▨		TD	1.00	1.00	0.00	32.21	C
▨		▨	▨	TD	0.64	-0.78	0.43	32.52	D
▨		▨		P	0.82	0.09	0.27	32.65	D
▨	▨		▨	TD	1.00	1.00	0.00	32.67	A
▨	▨		▨	TD	1.00	1.00	0.00	32.67	B
▨	▨		▨	TD	1.00	1.00	0.00	32.67	C
	▨	▨	▨	TD	0.74	-0.30	0.24	32.92	D
▨		▨		P	1.00	1.00	0.00	33.09	A
▨		▨		P	1.00	1.00	0.00	33.09	B
▨		▨		P	1.00	1.00	0.00	33.09	C

▨	▨	▨	▨	F	1.00	1.00	0.00	33.12	A
▨	▨	▨	▨	F	1.00	1.00	0.00	33.12	B
▨	▨	▨	▨	F	1.00	1.00	0.00	33.12	C
▨	▨	▨		P	1.00	1.00	0.00	33.25	A
▨	▨	▨		P	1.00	1.00	0.00	33.25	B
▨	▨	▨		P	1.00	1.00	0.00	33.25	C
▨	▨	▨	▨	TD	0.62	-0.99	0.41	33.49	D
▨		▨	▨	F	1.00	1.00	0.00	33.55	A
▨		▨	▨	F	1.00	1.00	0.00	33.55	B
▨		▨	▨	F	1.00	1.00	0.00	33.55	C
	▨	▨	▨	TD	1.00	1.00	0.00	34.08	B
	▨	▨	▨	TD	1.00	1.00	0.00	34.08	C
	▨	▨	▨	TD	1.00	1.00	0.00	34.08	A
	▨		▨	F	1.00	1.00	0.00	34.23	B
	▨		▨	F	1.00	1.00	0.00	34.23	C
	▨		▨	F	1.00	1.00	0.00	34.23	A
	▨	▨		F	1.00	1.00	0.00	35.13	A
	▨	▨		F	1.00	1.00	0.00	35.13	B
	▨	▨		F	1.00	1.00	0.00	35.13	C
	▨		▨	F	0.72	-0.38	0.39	35.51	D

	■	■		F	0.75	-0.24	0.33	35.52	D
■		■		F	0.83	0.17	0.14	35.61	D
■			■	F	0.77	-0.13	0.29	36.02	D
■	■		■	F	1.00	1.00	0.00	36.09	A
■	■		■	F	1.00	1.00	0.00	36.09	B
■	■		■	F	1.00	1.00	0.00	36.09	C
■			■	F	1.00	1.00	0.00	36.22	A
■			■	F	1.00	1.00	0.00	36.22	B
■			■	F	1.00	1.00	0.00	36.22	C
■	■	■		F	1.00	1.00	0.00	36.30	A
■	■	■		F	1.00	1.00	0.00	36.30	B
■	■	■		F	1.00	1.00	0.00	36.30	C
■		■	■	M	1.00	1.00	0.00	36.80	C
■		■	■	M	1.00	1.00	0.00	36.80	A
■		■	■	M	1.00	1.00	0.00	36.80	B
■	■	■		F	0.69	-0.54	0.33	36.83	D
■		■		F	1.00	1.00	0.00	37.15	A
■		■		F	1.00	1.00	0.00	37.15	B
■		■		F	1.00	1.00	0.00	37.15	C
■	■		■	F	0.68	-0.62	0.36	37.31	D

	■	■		P	0.83	0.17	0.14	37.48	D
	■	■	■	F	0.72	-0.38	0.26	37.51	D
■		■	■	F	0.63	-0.87	0.46	37.58	D
	■	■	■	F	1.00	1.00	0.00	38.22	A
	■	■	■	F	1.00	1.00	0.00	38.22	C
	■	■	■	F	1.00	1.00	0.00	38.22	B
■		■		M	0.85	0.23	0.10	38.45	D
■	■	■	■	M	1.00	1.00	0.00	38.50	C
■	■	■	■	M	1.00	1.00	0.00	38.50	A
■	■	■	■	M	1.00	1.00	0.00	38.50	B
■	■	■	■	F	0.59	-1.16	0.47	38.63	D
	■	■		P	1.00	1.00	0.00	39.04	A
	■	■		P	1.00	1.00	0.00	39.04	B
	■	■		P	1.00	1.00	0.00	39.04	C
■			■	M	1.00	1.00	0.00	39.04	C
■			■	M	1.00	1.00	0.00	39.04	A
■			■	M	1.00	1.00	0.00	39.04	B
	■	■		M	0.81	0.03	0.22	39.06	D
	■		■	M	0.77	-0.15	0.30	39.24	D
	■		■	M	1.00	1.00	0.00	39.31	A

	▨		▨	M	1.00	1.00	0.00	39.31	B
	▨		▨	M	1.00	1.00	0.00	39.31	C
▨			▨	M	0.75	-0.23	0.33	39.39	D
	▨	▨		M	1.00	1.00	0.00	40.03	A
	▨	▨		M	1.00	1.00	0.00	40.03	B
	▨	▨		M	1.00	1.00	0.00	40.03	C
▨	▨	▨		M	0.74	-0.32	0.24	40.19	D
▨		▨		M	1.00	1.00	0.00	40.22	A
▨		▨		M	1.00	1.00	0.00	40.22	B
▨		▨		M	1.00	1.00	0.00	40.22	C
▨		▨	▨	M	0.63	-0.84	0.45	40.44	D
▨	▨		▨	M	1.00	1.00	0.00	40.66	A
▨	▨		▨	M	1.00	1.00	0.00	40.66	B
▨	▨		▨	M	1.00	1.00	0.00	40.66	C
	▨	▨	▨	M	0.76	–0.18	0.18	40.97	D
▨	▨		▨	M	0.69	–0.55	0.33	41.23	D
▨	▨	▨		M	1.00	1.00	0.00	41.24	A
▨	▨	▨		M	1.00	1.00	0.00	41.24	B
▨	▨	▨		M	1.00	1.00	0.00	41.24	C
▨	▨	▨	▨	M	0.61	–1.06	0.42	42.13	D

	M	1.00	1.00	0.00	42.90	A
	M	1.00	1.00	0.00	42.90	B
	M	1.00	1.00	0.00	42.90	C

Table S5.3: Statistical estimates of the second-best and third-best models in the path analysis. An arrow with a single arrowhead indicates regression. SST, sea surface temperature; SOJ, Sea of Japan; PO, Pacific Ocean; S.E., standard error; *Z*, z value; *P,* P-value

The second-best model

Parameter Estimate	Estimate	S.E.	*Z*	*P*
probability of entering the PO ← mean of SST in the SOJ	–0.039	0.037	–1.07	0.29
probability of entering the PO ← coefficient of variation of SST (SOJ)	–0.51	0.19	–2.69	0.007
probability of entering the PO ← coefficient of variation of SST (PO)	1.22	0.19	6.38	0.000
probability of entering the PO ← chick growth rate				
Error variable [probability of entering the PO]	–0.14	0.037	–3.80	0.000

The third-best model

Parameter Estimate	Estimate	S.E.	*Z*	*P*
probability of entering the PO ←coefficient of variation of SST (SOJ)	–0.50	0.19	–2.68	0.007
probability of entering the PO ← mean of SST (PO)	–0.039	0.032	–1.22	0.22
probability of entering the PO ←coefficient of variation of SST (PO)	1.15	0.16	7.43	0.000
Error variable [probability of entering the PO]	–0.12	0.033	–3.73	0.000

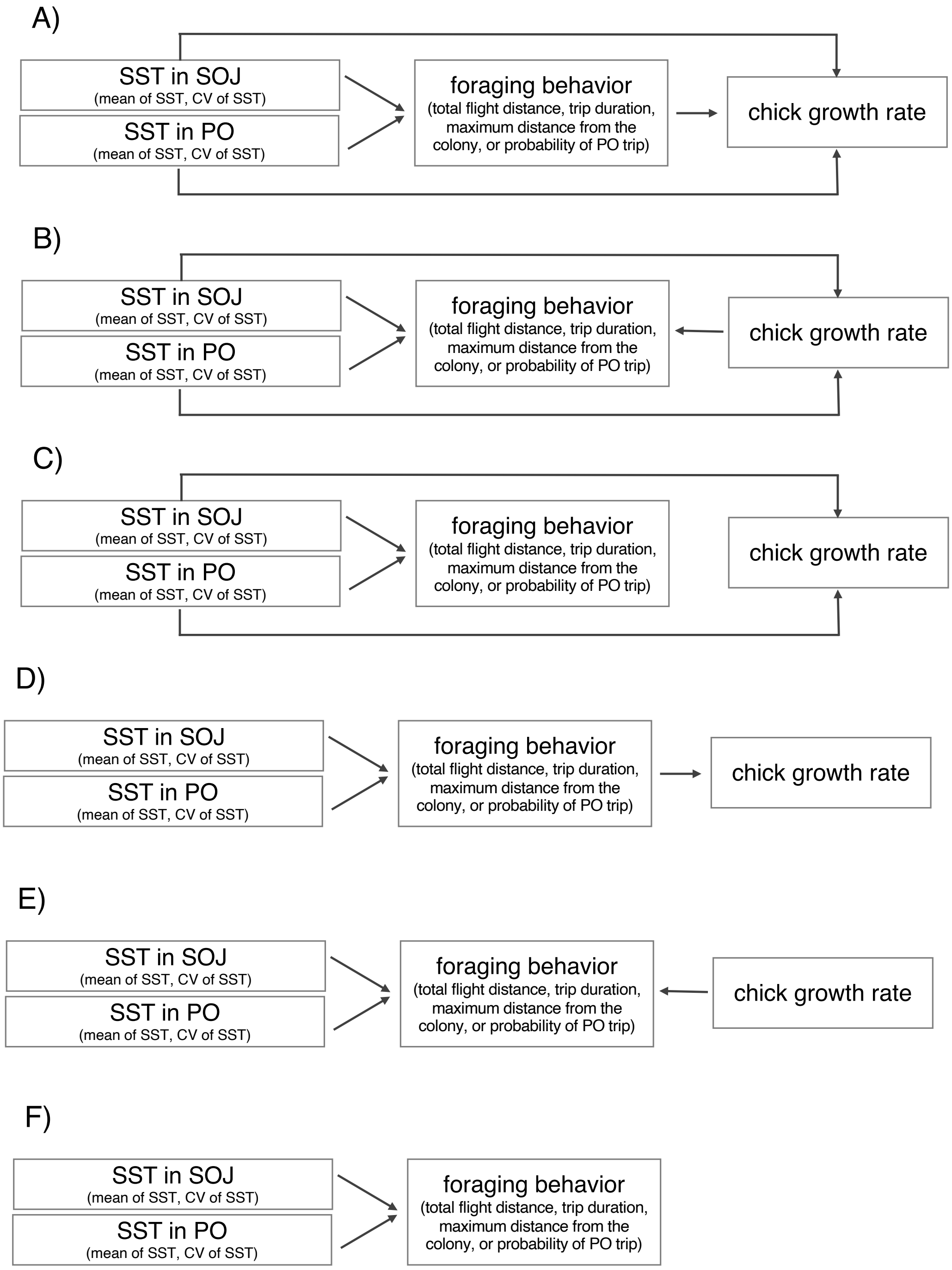


Figure S5.1: Models that we have constructed to examine the relationships between SST, foraging parameter, and chick growth. sea surface temperature; SST, the Sea of Japan; SOJ, the Pacific Ocean; PO, coefficient of variation; CV

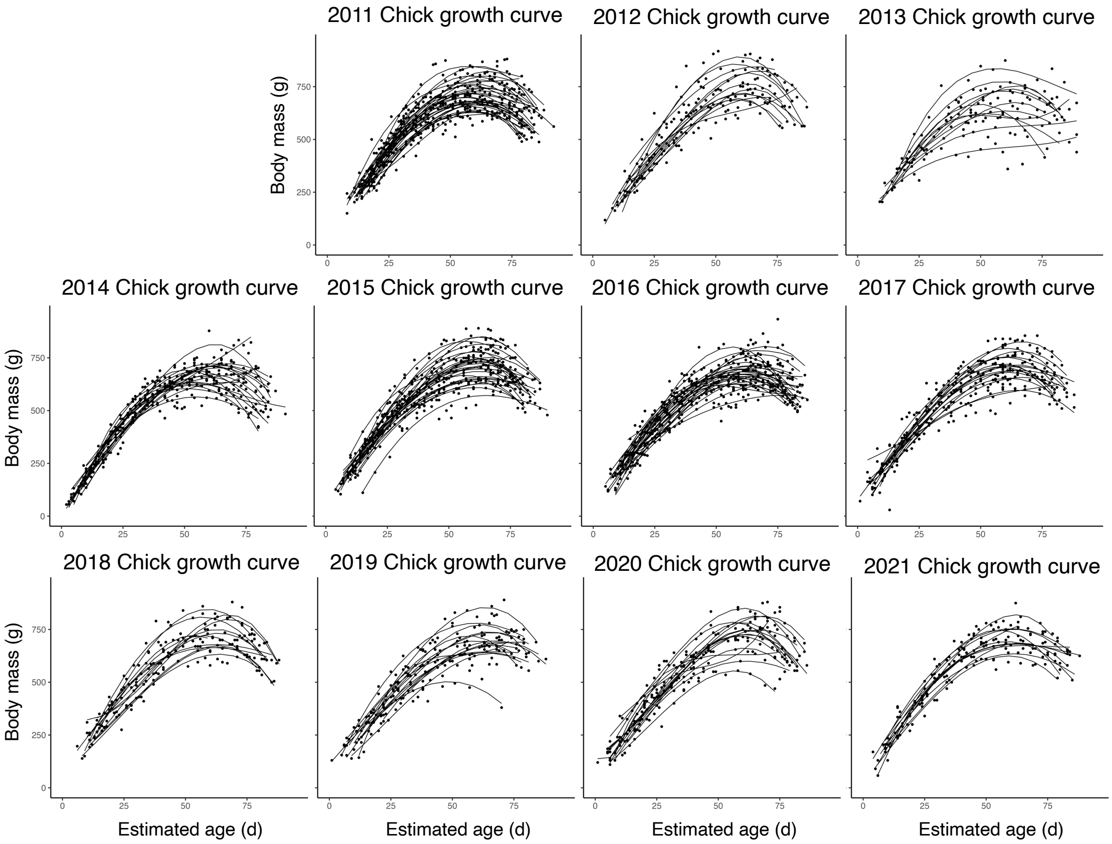


Figure S5.2. Chick growth curve of each year. The dots show the recorded body mass. The black lines show the growth curves of individual. Individual number were 32 in 2011, 13 in 2012, 12 in 2013, 20 in 2014, 27 in 2015, 28 in 2016, 17 in 2017, 13 in 2018, 16 in 2019, 16 in 2020, and 13 in 2021.

Chapter 6. General discussion

In chapters 3 to 5, I have demonstrated that 1) oxidative stress can be used as an indicator of physiological fatigue caused by forging movement and recovery capacity from the fatigue caused by obtaining food; 2) foraging of seabirds was influenced by other marine predators, physical oceanographic features, and demand from chicks.

6.1. Advantages and disadvantage of methods to measure physiological costs associated with foraging behavior of seabird

Oxidative stress measurements are useful because they quantify not only the physiological fatigue associated with foraging behavior, but also the capacity of recovery from the foraging-induced fatigue. Other than oxidative stress measurement, there are four main techniques for measuring physiological costs associated with foraging behavior of seabirds: the DLW method, the heart rate method, the ODBA method, and measurement of baseline of corticosterone (CORT) (Halsey et al., 2011, Table 6.1). The DLW method has the disadvantages of being either expensive (Butler et al., 2004) or requiring the individual to be recaptured of the individual before all isotopes are emitted, and thus, is not suitable for quantifying the physiological cost of long-duration excursions by seabirds (measurable durations are 2 days; Shirai et al., 2015). The heart rate method measuring approach calculates the oxygen consumption by using heart rate loggers (Green 2011; Viblanc et al., 2011) and behavior-recording loggers (Hicks et al., 2017). However, attaching several loggers to small and semi-sized seabirds within the weight restriction of loggers (less than 5% of body mass) is problematic. Moreover, my research found that higher ODBA levels, which may increase the metabolic rate (Wilson et al., 2006) and the heart rate (Hicks et al., 2017), may lower the oxidative stress by consuming food rich in antioxidants. Thus, DLW and heart rate methods may overlook or undervalue the advantage of foraging and obtaining food. Baseline CORT level in plasmas is used to quantify the physiological cost involved in foraging behavior decisions (Angelier et al., 2007b; Angelier et al.,2008; Cottin et al., 2011; Crossin et al., 2012; Cottin et al., 2014; Kroeger et al., 2019), surrounding environment (Laranjeiro et al., 2020), and food acquisition (Angelier et al., 2007a; Angelier et al. 2008; Fairhurst et al., 2011). CORT baseline and oxidative stress are closely related, i.e., oxidative stress increases CORT baseline by inhibiting regulation systems that release CORT (Vitale et al., 2013), and CORT increase oxidative stress, as demonstrated by CORT implantation studies (Lin et al., 2004; Costantini et al., 2011; Haussmann et al., 2012). Therefore, CORT baseline may reflect oxidative damage in the body to some degree. By quantifying pro-oxidant, a direct index of bio-molecules damage from respiration, and antioxidant from food, an index of the capacity of recovery from the fatigue, oxidative stress measurements provide higher resolution quantification of the physiological cost associated with foraging behavior.

6.2 Little intra- and inter-specific competition in foraging sites

The inter- and intra-specific relationships in marine animals are poorly understood as compared to terrestrial animals. Some studies indicate that spatial habitat segmentation or specialization of marine predators occurs in stable environments because of competitive exclusion and site favor (Ceia & Ramos 2015; Bolton et al., 2019; Table 6.4), whereas others indicate that marine predators gather in the same feeding sites in the environment with low food availability and uneven distribution of resource (Veit & Harrison, 2017; Dehnhard et al., 2020). Streaked shearwaters foraged in the same location as common dolphinfish without competing (chapter 4), and they chose their foraging sites in response to the changing physical environment annually (chapter 5). The video loggers did not record direct exclusion behavior occurring among streaked shearwaters gathering at the same feeding site in the SOJ, which has lower food availability as compared to the PO (Qiu 2019; Lee et al., 2019; Figure 6.1). These results indicated that streaked shearwaters might not compete with common dolphinfish or other individuals of the same species in foraging sites, and no evident specialization of feeding sites on annual basis. In an unevenly distributed food environment, seabirds sharing their foraging site with other marine top predators may not change their distribution significantly due to competitive exclusion from other intra- and inter-specific (Dehnhard et al., 2020). Individuals would fly farther and longer to search for prey if competition or a lack of prey occurred in seabirds, increasing their oxidative stress (chapter 3), decreasing reproductive success (Costantini & Dell'Omo, 2015; Montoya et al., 2016; Merkling et al., 2017; Table 6.2) or survival probability (Noguera et al., 2012; Costantini & Dell'Omo, 2015; Herborn et al., 2016), and ultimately leading to population decline.

6.3 Surrounding environment, foraging behavior, oxidative stress, and reproduction

Streaked shearwaters might prefer foraging in the PO, because of the high food availability. In contrast, I discovered that in years when streaked shearwaters flew frequently to the PO, they increased their pro-oxidant levels increased due to flying farther from the colony. Differences in prey species could explain this disparity (Beaulieu 2010; Beaulieu et al., 2015; Laranjeiro et al., 2020). When the food availability for streaked shearwaters is low, high variability of SST in the PO might indicate the presence of Japanese anchovies rather than Pacific saury, which is a high-energy prey for streaked shearwaters (Kurasawa et al., 2011; Ochi et al., 2016; note that selenium, antioxidant materials, in Japanese anchovy and Pacific in a mass unit saury are not significantly different; Yamashita et al., 2011). In a such year, streaked shearwaters might be unable to obtain prey with sufficient antioxidants to recover from the fatigue of the long-distance travel. It suggests the possibility that streaked shearwaters might not select their foraging sites based on the prey species. The presence of other predators might attract streaked shearwaters, which are more likely to reflect the amount of food available rather than the prey species.

According to my findings, yearly differences in the parameters of foraging behavior of streaked shearwaters and parental behavior did not explain chick growth rate (chapter 5). They might be able to mitigate the effect of environmental change by flexibly modifying their foraging behavior in response to the surrounding environment and demands from their offspring (Elliott et al., 2014; Dehnhard et al., 2016; Christensen-Dalsgaard et al., 2018; Table 6.3 and Table 6.4). Moreover, I discovered no significantly yearly difference in the changes of pro-oxidants and antioxidants levels, despite the fluctuations in food availability were suggested (Appendix 3.6). Streaked shearwaters might maintain a favorable physiological condition in preferable level thorough behavioral or physiological buffering, while the physiological cost is influenced by their foraging behavior (Grémillet et al., 2012; Kidawa et al., 2017; Schoen et al., 2018). These findings corroborate the general notion that wild animals evolve to adapt to new habitats on an annual basis while maintaining some level of physiological condition and current reproductive success.

In conclusion, streaked shearwaters determined foraging site based on the surrounding environment, SST variability, the presence of other predators, and chick demands. Long distance trips and frequency of takeoffs from the sea surface increased their oxidative stress, whereas food acquisition decreased their oxidative stress. By modifying their foraging site or behavior, streaked shearwaters may be able to mitigate the impact of shifting food availability on chick growth and maybe on their own physical condition (Figure 6.2). This evidence suggests that long-lived seabirds can adapt to changing environment while maintain some degree of physiological condition and current reproductive performance thorough their flexible foraging behavior (Weimerskirch et al., 1995). This adaptable foraging behavior and ability to buffer environmental influences may be enabled by behavioral traits such as taking a variety of foraging trip durations and having the ability to forage in high food availability areas, as well as reproductive traits such as raising one chick with slow development (Granadeiro et al., 1998; Schultz & Klomp, 2000; Baduini & Hyrenbach, 2003).

6.5. Tables and figures

Table 6.1: Overview of studies demonstrating the relationship between baseline plasma CORT (b-CORT) and foraging behavior in wild seabirds. I; incubation period, Bro.; Brooding period, R; chick rearing period, Bre.; breeding period, +; positive effect, −; negative effect, N.S.; no significant. *1: CORT implant treatment

species	individual	explanatory variable	response variable	result	reference
wandering albatross (*Diomedea exulans*)	adult (I)	mass gain	b-CORT post-trip	−	Angelier et al. 2007a
	adult (I)	b-CORT pre-trip	foraging distance	+	
black-legged kittiwake (*Rissa tridactyla*)	male adult (R)	CORT implant	flying/foraging time	control < treated	Angelier et al. 2007b
	male adult (R)	CORT implant	mass gain	control < treated	
Adélie penguin (*Pygoscelis adeliae*)	adult (Bro.)	b-CORT pre-trip	time at sea	−	Angelier et al. 2008
	adult (Bro.)	b-CORT pre-trip	mass gain	−	
	adult (Bro.)	b-CORT pre-trip	foraging distance	−	
	adult (Bro.)	b-CORT pre-trip	change of CORT	−	
least auklet (*Aethia pusilla*)	adult (Bro.)	year	b-CORT	N.S.	Benowitz-Fredericks et al. 2008

thick-billed murre (*Uria lomvia*)	adult (Bre.)	year	b-CORT	2003 < 2004	
auklet/murre	adult (Bre.)	species	b-CORT	auklet > murres	
macaroni penguin (*Eudyptes chrysolophus*)	female adult (R)[*1]	b-CORT post-trip	dive number	+	Crossin et al., 2012
	female adult (R)[*1]	b-CORT post-trip	time spent diving	+	
	female adult (R)[*1]	b-CORT post-trip	mass gain	+	
	female adult (R)[*1]	b-CORT post-trip	chick mass	+	
thick-billed murre (*Uria lomvia*)	adult (Bre.)	colony, prey	b-CORT	colony	Harding et al., 2013
Adélie penguin (*Pygoscelis adeliae*)	male adult (R)	CORT implant	diving behavior	control < treated	Cottin et al., 2014
thick-billed murre (*Uria lomvia*)	adult (R)	temperature	b-CORT	−	Kokubun et al., 2018
	male adult (R)	b-CORT	proportion of dives	+	
Campbell albatross (*Thalassarche impavida*)	adult (I)	b-CORT pre-trip	mass gain	+	Kroeger et al., 2019
gray-headed albatross (*Thalassarche chrysostoma*)	adult (I)	b-CORT pre-trip	mass gain	+	
Campbell albatross	adult (R)	b-CORT pre-trip	mass gain	+	
	adult (R)	mass gain	change of b-CORT	−	

Table 6.2: Overview of oxidative stress associated with reproduction and foraging of seabirds. I; incubation period, R; chick rearing period, B; breeding period C; courtship, OS; oxidative stress, D; oxidative damage, A; antioxidants, ROS; reactive oxygen species, SOD; superoxide dismutase, LP; lipid peroxidation, GPx; glutathione peroxidase, UA; uric acid, +; positive effect, −; negative effect, N.S.; no significant. *1; d-ROMs assay, *2; TBARS assay, *3; OXY assay, *4; OS parameters are measured using red blood cells. OS parameters without park (*4) measured by using plasma samples.

species	individual	OS parameter	related parameter	result	reference
streaked shearwater (*Calonectris leucomelas*)	adult (R)	ROS (D)^{*1}	maximum range of trip (in 2019)	+	this study
	adult (R)	ROS (D)^{*1}	number of takeoffs (in 2019)	+	
	adult (R)	antioxidants (A)	ODBA (in 2018)	+	
Adélie penguin (*Pygoscelis adeliae*)	adult (R)	ROS (D)^{*1}	δ13C	+	Beaulieu et al., 2010
European shag (*Phalacrocorax aristotelis*)	nestlings	LP (D)	resight probability	−	Noguera et al., 2012
wandering albatross (*Diomedea exulans*)	adult	LP (D)^{*2}	breeding status	non-B < B	Costantini et al., 2014
	adult (non-B)	LP (D)^{*2}	age	+	

gentoo penguin (*Pygoscelis papua*)	adult (R)	ROS (D)^{*1}	δ13C, δ15N	+	Beaulieu et al., 2015
Scopoli's shearwater (*Calonectris diomedea*)	adult (B)	ROS (D)^{*1}	resight probability	−	Costantini & Dell’Omo, 2015
	adult (B)	ROS (D)^{*1}	number of chicks	−	
wandering albatross (*Diomedea exulans*)	adult male (non-B)	LP (D)^{*2}	breeding probabilities	−	Costantini et al., 2015
	adult (non-B)	LP (D)^{*2}	breeding success	N.S.	
	adult (non-B)	LP (D)^{*2}	resight probability	N.S.	
European shag (*Phalacrocorax aristotelis*)	adult (B)	ROS (D)^{*1}	resight probability	−	Herborn et al., 2016
	chick	ROS (D)^{*1}	resight probability	−	
brown booby (*Sula leucogaster*)	adult female (C)	ROS (D)	first eggs volume	−	Montoya et al., 2016
	adult (C)	ROS (D)	breeding status	C > R	
	adult (C)	LP (D)^{*2}	chick LP level	+	
Magellanic penguin (*Spheniscus magellanicus*)	adult	antioxidants (A)^{*3}	breeding status	I < R	Colominas-Ciuró et al., 2017
black-legged kittiwake (*Rissa tridactyla*)	adult (pre-I)	SOD (A)^{*4}	days spent chicks	−	Merkling et al., 2017

little auk (*Alle alle*)	adult	ROS (D)[*1]	breeding status	I > R	Kulaszewicz et al., 2018
yellow-legged gull (*Larus michahellis*)	adult (B)	DNA damage[*4]	Colony		Laranjeiro et al., 2020
Y. gull /Audouin's gull (*Larus audouinii*)	adult (B)	LP (D)[*2*4]	Species	Y. gull > A. gull	
Scopoli's shearwater (*Calonectris diomedea*)	adult	antioxidants (A)[*3]	breeding status	I > R	Colominas-Ciuró et al., 2022a
Magellanic penguin (*Spheniscus magellanicus*)	adult (R)	α-tocopherol (A)	sex	male > female	Colominas-Ciuró et al., 2022b
thick-billed murre (*Uria lomvia*)	adult (B)	antioxidants (A)	sex	male < female	Lin et al., 2022

Table 6.3: Overview of observational studies demonstrating causal relationship between chick demands (explanatory variable) to parental behavioral in subsequent trip (response variable) in Procellariiformes. LT; long trip, ST; short trip (see each reference for definitions of LT and ST), +; positive effect, −; negative effect, N.S.; no significant, x; mixed effect, PO; Pacific Ocean. *1; female=0, male=1, *2; PC1 value from trip parameters.

species	explanatory variable	response variable	effect	reference
streaked shearwater (*Calonectris leucomelas*)	chick growth	probability entering the PO	+	This study
Cory's shearwater (*Calonectris borealis*)	chick body condition	meal mass	N.S.	Hamer & Hill, 1993
little shearwater (*Puffinus assirnilis*)	chick body condition	meal mass feeding frequency	N.S. N.S	Hamer, 1994
sooty shearwater (*Puffinus griseus*)	adult mass	short trip probability	+	Weimerskirch, 1998
	meal size		N.S.	
	previous foraging trip duration		N.S.	
	chick body condition		N.S.	
	time last meal received by chick		N.S.	
	adult mass x previous trip duration		N.S.	

white-chinned petrel (*Procellaria aequinoctialis*)	chick body condition	meal mass	−	Catard et al., 2000
		start ST or LT	N.S.	
		trip duration	N.S.	
black-browed albatross (*Thalassarche melanophris*)	chick body condition	trip duration	+	Phillips et al., 2009
		maximum range	N.S.	
		meal mass	−	
grey-headed albatross (*Diomedea chrysostoma*)	chick body condition	trip duration	N.S.	
		maximum range	N.S.	
		meal mass	N.S.	
light-mantled albatross (*Phoebetria palpebrata*)	chick body condition	trip duration	N.S.	
		maximum range	N.S.	
		meal mass	N.S.	
streaked shearwater (*Calonectris leucomelas*)	parental body condition	trip duration	−	Ochi et al., 2010
	chick body condition	trip duration	+	
	parental sex[*1]	trip duration	+	
	chick age	trip duration	N.S.	
	parental body condition x sex[*1]	trip duration	+	
	parental sex x chick age	trip duration	−	

Cory’s shearwater	primary productivity	LT trip	−	Cecere et al., 2014
(*Calonectris borealis*)	chick body mass	LT trip	+	
Manx shearwater	adult body condition	trip duration and distance^{*2}	N.S.	Wischnewski et al., 2019
(*Puffinus puffinus*)	chick body condition	trip duration and distance^{*2}	+	

Table 6.4: Overview of multi-year studies evaluating SST (food availability), foraging behavior, and reproductive performance in Procellariiformes. Symbols in brackets indicate changes in SST, behavior, and reproductive performance (↑ ; increase, ↓ ; decrease, N.S.; no significant changes). SST; sea surface temperature, NPGO; North Pacific Gyre Oscillation index. *1; El Niño and La Niña conditions

species	SST	behavior	chick	years	reference
yellow-nosed albatross (*Thalassarche chlororhynchos*)	anomalies (↑)	trip duration (↑)	body mass (↓) fledging success (N.S.)	5	Weimerskirch et al., 2001
wedge-tailed shearwater (*Puffinus pacificus*)	mean (↑)	feeding frequency (↓)	body mass (↓)	2	Smithers et al., 2003
yellow-nosed albatross (*Thalassarche chlororhynchos*)	front position (father)	trip distance (↑)	body mass (↓) wing length (N.S.)	2	Pinaud et al., 2005
short-tailed shearwater (*Puffinus tenuirostris*)	mean (↑)	feeding frequency (↓)	breeding success (N.S.)	3	Einoder et al., 2013

short-tailed shearwater (*Puffinus tenuirostris*)	mean (↑)	trip distance (↑)	breeding success (↓)	3	Berlincourt & Arnould, 2015
Laysan albatross (*Phoebastria immutabilis*)	front position (father)[*1]	trip duration and distance (↑)	reproductive success (↓)	10	Thorne et al., 2015
black-footed albatross (*Phoebastria nigripes*)	NPGO (↑)[*1]	trip distance (↑)	reproductive success (↓)		
common diving petrel (*Pelecanoides urinatrix*)	mean (↑)	trip duration and distance (↑)	breeding success (↓)	4	Fromant et al., 2021

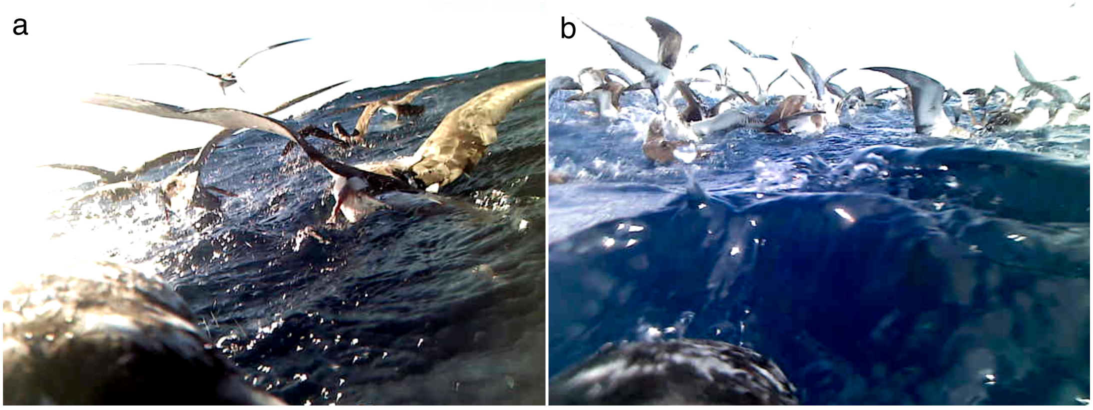


Figure 6.1: Screenshots taken by video logger. Snapshot (a) was taken at 7:50 a.m. on September 21st, 2021 (local time, JST) at 40◦24′ N, 139◦51′ E. Snapshot (b) was probably taken around 0 p.m. on September 18th, 2022 (local time, JST) around 39◦16′ N, 139◦13′ E (the video logger failed to record accurate time and location). A head of streaked shearwaters is shown at the bottom of screenshots (a) and (b). Streaked shearwaters gather at the same foraging site without engaging in competitive behavior. All of the movies that captured the screenshots featured common dolphinfish.

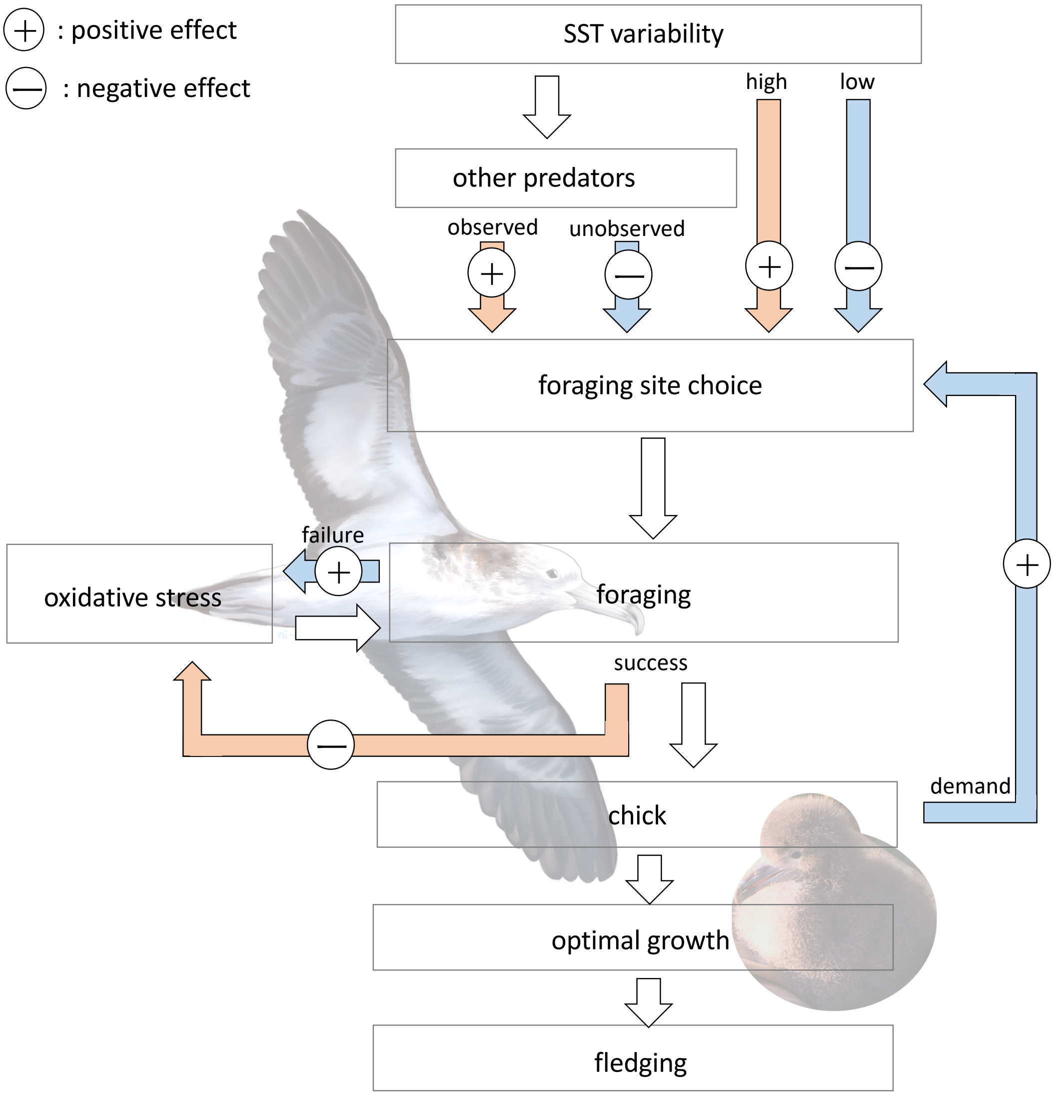


Figure 6.2: Diagram of the demonstrated relationship between environment, behavior, physiological condition, and reproductive performance demonstrated in this thesis. The red and blue arrows represent scenarios with good and adequate food availability environment, respectively. White arrows represent potential causal relationships.

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