Corticosterone and Foraging Behavior in a Pelagic Seabird

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ABSTRACT

Because endocrine mechanisms are thought to mediate behavioral responses to changes in the environment, examining these mechanisms is essential for understanding how long-lived seabirds adjust their foraging decisions to contrasting environmental conditions in order to maximize their fitness. In this context, the hormone corticosterone (CORT) deserves specific attention because of its major connections with locomotor activities. We examined for the first time the relationships between individual CORT levels and measurements of foraging success and behavior using satellite tracking and blood sampling from wandering albatrosses (*Diomedea exulans*) before (pretrip CORT levels) and after (posttrip CORT levels) foraging trips during the incubation period. Plasma CORT levels decreased after a foraging trip, and the level of posttrip CORT was negatively correlated with individual foraging success, calculated as total mass gain over a foraging trip. Pretrip CORT levels were not linked to time spent at sea but were positively correlated with daily distance traveled and maximum range at sea. In this study, we were able to highlight the sensitivity of CORT levels to variation in energy intake, and we showed for the first time that individual CORT levels can be explained by variation in foraging success. Relationships between pretrip CORT levels and daily distance traveled and maximum range were independent of pretrip body mass, suggesting that slight elevations in pretrip CORT levels might facilitate locomotor activity. However, because both foraging behavior and pretrip CORT levels could be affected by individual quality, future experimental studies including manipulation of CORT levels are needed to

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test whether CORT can mediate foraging decisions according to foraging conditions.

Introduction

During breeding, the ability of individuals to adjust energy expenditure while foraging is likely to influence fitness (Stephens and Krebs 1986) because foraging effort and success determine the amount of resources that can be allocated to fitness-related activities (van Noordwijk and de Jong 1986). Because long-lived organisms should behave as prudent parents (Drent and Daan 1980), they should adjust their foraging effort in relation to environmental conditions in order to maximize current reproduction without compromising survival and future reproductions (Stearns 1992). For instance, long-lived seabirds should reduce their investment in reproduction with increasing foraging costs because of their high residual reproductive value (Costa 1991; Boggs 1992; Weimerskirch 1999; Weimerskirch et al. 2001, 2003). Because endocrine mechanisms are thought to mediate physiological and behavioral responses to variations of the environment (Ricklefs and Wikelski 2002), examining endocrine mechanisms that govern foraging decisions is essential for exploring life-history trade-offs (Sinervo and Svensson 1998) and especially for understanding how long-lived seabirds adapt their foraging decisions to the environment in order to maximize their fitness.

In this context, focusing on corticosterone (CORT) is especially judicious when examining foraging behavior because this hormone is considered as the primary mediator of allostasis in birds and functions to mobilize energy stores and adjust behavior and physiology appropriately to the conditions encountered (review in McEwen and Wingfield 2003; Landys et al. 2006). Despite the commonly held opinion that having high CORT levels over a prolonged time is inhibitory to reproductive function, there is growing evidence that temporary elevation in baseline CORT levels is indeed inherent and necessary for successful reproduction (Moore and Jessop 2003; Love et al. 2004). For example, elevated baseline levels have been correlated with the increased energetic demand of raising offspring (Silverin 1982; Kitaysky et al. 1999; Romero 2002; Love et al. 2004; Chastel et al. 2005) or with a change in activity budget of breeding individuals during stressful events (Kitaysky et al. 2001). The idea that slight or temporary increases in CORT levels—below those that induce nest desertion (Silverin 1986; Cherel et al. 1988)—may indeed promote breeding investment through short-term behavioral and physiological adjustments

becomes evident when considering the causal link between CORT and foraging: elevated baseline CORT levels might increase locomotor activity (Astheimer et al. 1992; Challet et al. 1995; Breuner and Wingfield 2000), foraging behavior during migration (Wingfield et al. 1990), time spent foraging (Kitaysky et al. 2001), and food intake rate (Deviche and Schepers 1984; Astheimer et al. 1992). To our knowledge, however, no study has measured the relationships between individual CORT levels and accurate measurements of foraging behavior and success in large free-ranging animals.

The recent development of miniaturized Argos telemetry, GPS systems, and bird-borne activity loggers (Jouventin and Weimerskirch 1990; Weimerskirch et al. 1994, 2002; Wilson et al. 1995; Shaffer et al. 2003; Phillips et al. 2004) has allowed the collection of detailed information on foraging areas, activity at sea, and foraging efficiency for several species of albatrosses and petrels (order Procellariiformes). In these pelagic seabirds, breeding grounds and prey resources are often separated by considerable distances (Pennycuick et al. 1984; Jouventin and Weimerskirch 1990; Ricklefs 1990). During the incubation stage, adults alternate between foraging episodes at sea and periods of prolonged fasting on the nest. Fasting places a major constraint on the foraging decisions of adults because foraging success (i.e., mass gain at sea) will have a profound impact on the ability of a bird to fast and incubate successfully (Chastel et al. 1995a, 1995b). It is likely that short-term adjustments in foraging effort are adopted by adults to cope with variations in food supply and that this is influenced by changes in baseline CORT levels elicited during the previous incubation bout. Because CORT is known to be associated with both protein catabolism in fasting birds (Le Ninan et al. 1988) and fat deposition in foraging migratory birds (Holberton 1999), the relationship between CORT and foraging success is unclear and thus deserves further examination. In pelagic seabirds that rely on patchy ephemeral prey, foraging success can be highly variable, so it is likely that CORT levels change concomitantly with mass gain and hence food availability. The possibility of measuring foraging behavior and success of albatrosses and petrels during the incubation period (Shaffer et al. 2001, 2003; Weimerskirch et al. 2003) makes these pelagic seabirds promising models to study the interrelationships between body mass, CORT levels, and foraging behavior and success.

Therefore, the aim of this article is to examine in a pelagic seabird, the wandering albatross (*Diomedea exulans*), (1) how foraging success affects plasma levels of CORT in albatrosses returning from a foraging trip (posttrip CORT levels) and (2) how CORT levels measured before a foraging trip (pretrip CORT levels) might influence specific components of foraging behavior obtained using satellite transmitters. Because baseline CORT levels are known to be negatively correlated with food abundance in seabirds (Kitaysky et al. 1999), we predict that foraging success (total mass gain over a foraging trip) negatively affects plasma levels of posttrip CORT. Moreover, because

CORT is known to facilitate locomotor activity (review in Wingfield et al. 1998), we predict that pretrip CORT levels are positively correlated with daily distance traveled and maximum range (which reflect foraging intensity; Weimerskirch et al. 2005).

Material and Methods

This study was conducted during the austral summer of 1999 on Possession Island, Crozet Archipelago, southwestern Indian Ocean (46°S, 52°E). Sixteen wandering albatrosses (11 males and five females) were studied from mid-January to early February during the incubation period. In wandering albatrosses, the incubation period lasts for about 78 d, during which males and females alternate incubation spells lasting 11–13 d on average. Incubating wandering albatrosses can fast for up to 38 d and can lose a significant portion of their body mass (up to 20%–30%, average 11%) during an incubation shift (Weimerskirch 1995, 1999). After their incubation duty, birds forage over huge distances and follow a looping course ranging in all directions as far as the Antarctic waters and the subtropical waters (Jouventin and Weimerskirch 1990). Wandering albatrosses rely on prey that has a patchy and unpredictable distribution (Ashmole 1971), and their long-distance foraging strategy allows them to maximize the area prospected per unit of time (Weimerskirch et al. 1997).

Blood Sampling and Hormone Assays

Birds were captured by hand off the nest, and sex was determined by plumage characteristics (Weimerskirch et al. 1989). Birds were sampled on two occasions. First, blood samples were collected when birds were about to head to sea, exactly at the moment they were leaving the nest (pretrip CORT: CORT measured before a foraging trip, $N = 16$ blood samples). Nests were then observed daily (from dawn to dusk) until the birds returned to their nest. Second, blood samples were collected just after their return to start another incubation shift, immediately after they had relieved their partner and began to incubate the egg (posttrip CORT: CORT measured after a foraging trip, $N = 11$ blood samples). Eleven birds were sampled at both occasions, allowing for measurements of individual changes in CORT levels after a foraging trip. Each bird was weighed to the nearest 50 g using a Salter spring balance (Salter Weightronix, West Bromwich) before (pretrip body mass) and after (posttrip body mass) a trip to sea ($N = 16$), and mass difference was used as the index of foraging success. No birds abandoned their nest after capture and sampling; all returned from foraging and were seen incubating later in the breeding season.

A maximum of 1 mL of blood was collected from a tarsal vein into heparinized Eppendorf tubes and centrifuged for 10 min, and the plasma was removed and stored at −20°C until assayed for CORT levels. Blood samples were collected within

Table 1: Biological assumptions tested and associated generalized linear models

Biological Assumption	Dependent Variable	Independent Variables
Effect of foraging success on posttrip CORT level	Posttrip CORT level	Foraging success, date
Effect of pretrip CORT level on daily distance traveled	Daily distance traveled	Pretrip CORT, body mass, date
Effect of pretrip CORT level on time at sea	Time at sea	Pretrip CORT, body mass, date
Effect of pretrip CORT level on maximum range	Maximum range	Pretrip CORT, body mass, date, time at sea

Note. Model selection was performed by a step-down approach (Lebreton et al. 1992) using Akaike's Information Criterion and starting from the global model, including all the independent variables.

1–5 min. Plasma concentrations of total CORT were determined by radioimmunoassay following procedures described by Lormée et al. (2003). Minimum detectable CORT levels were 400 pg/mL. All plasma samples were processed in one assay. The intraassay variation was 5.3% ($N = 5$ duplicates). Because we found no relationship between handling time and CORT levels before or after a foraging trip (before: $F_{1,14} = 0.021$, $P = 0.65$; after: $F_{1,9} = 0.11$, $P = 0.75$), assayed levels of CORT were considered to reflect baseline levels of CORT. Moreover, baseline pretrip or posttrip CORT levels were not influenced by the time of the day when samples were collected (before: $F_{1,14} = 0.90$, $P = 0.36$; after: $F_{1,9} = 0.68$, $P = 0.43$).

At Sea Foraging Behavior and Activity Patterns

We monitored the time spent at sea to forage of each albatross ($N = 16$). In addition to blood sampling, the movement patterns of 14 albatrosses were studied using satellite platform terminal transmitters (PTTs; Pico-100, Microwave Telemetry, Columbia, MD). Birds were equipped with a 20–30-g PTT attached to feathers on the back with white adhesive tape. The PTTs transmitted a signal every 90 s, and six to 12 geographical locations were provided by Service Argos (CLS Argos, Toulouse) for each bird per day. Postprocessing of geographical locations was performed with ELSA software (CLS Argos) using standard Argos class designations (classes 0–3, A, and B) to evaluate the accuracy of locations. The data were manually filtered according to procedures described in Weimerskirch et al. (1993). For each foraging trip, we quantified the time at sea (d), daily distance traveled (km), and maximum range from colony (km). Maximum range was a measurement of the maximum distance from the colony.

Statistical Analyses

All analyses were performed with SAS statistical software (ver. 8.02; SAS Institute). Only one partner from each nest was studied so the data obtained from male and female albatrosses were considered independent samples. Each measured variable was tested for normality (Kolmogornov-Smirnov one-sample test), and no variable deviated from this assumption. Because there was no difference between sexes in CORT levels (Hector and Harvey 1986; this study) and foraging behaviors (Shaffer et al.

2001; this study), we pooled data from both sexes for subsequent analyses. However, because body mass was greater in males compared with females (Weimerskirch 1995; this study), we standardized body mass by subtracting the sexual mean body mass from each observed value and dividing by the standard deviation (Zar 1999). This statistical approach has been widely used to avoid potential confounding effects of a factor (i.e., sex in our study) on the relationship between two parameters, that is, body mass and either CORT levels or foraging parameters (Robertson and Rendell 2001; Laaksonen et al. 2002; Reid et al. 2003). In our study, this statistical approach allowed us to minimize the number of dependent variables in our generalized linear models (GLMs) and therefore to test the influence of body mass on variables to explain with a larger statistical power.

First, we focused on the functional mechanisms underlying individual variations in CORT levels during a foraging trip. We used paired Student's t-tests to examine how CORT levels changed after a foraging trip and linear regressions to test (1) whether pretrip and posttrip CORT levels varied with date and pretrip and posttrip body mass and (2) whether foraging success varied with date. We then used GLMs with normal errors and an identity link function (GENMOD procedure of SAS) to examine the influence of foraging success and date on posttrip CORT levels (Table 1). Second, we focused on the physiological mechanisms underlying components of foraging behavior. We used GLMs with normal errors and an identity link function to test the effect of pretrip CORT level, standardized pretrip body mass, and date on daily distance traveled, time at sea, and maximum range of the foraging trip (Table 1). Moreover, we used an r^2-like statistic for GLMs by using the analogy with error sums of squares (Myers and Montgomery 1997) in order to assess the percentage of variation in the dependent variable that is explained by independent variables:

$$\bar{r}^2 = \frac{\lambda(B_0) - \lambda(B)}{\lambda(B_0)},$$

where λ is the deviance associated with the intercept model (B_0) with the model used (B).

We used a second-order Akaike's Information Criterion (AICc) to select the most parsimonious model (Burnham and Anderson 2002) by following a step-down approach (Lebreton

Table 2: Plasma levels of baseline corticosterone (CORT), body mass, foraging success, and foraging parameters of male and female wandering albatrosses

| Parameters | Sex | | | | Statistical Test | |
	Male	N	Female	N	t	P
Pretrip CORT level (ng/mL)	10.47 ± 5.98	11	7.24 ± 6.17	5	−1.04	.32
Posttrip CORT level (ng/mL)	6.23 ± 3.36	7	3.84 ± 1.43	4	−1.64	.14
Pretrip body mass (kg)	9.56 ± .47	11	7.92 ± .46	5	−6.53	<.001
Posttrip body mass (kg)	10.90 ± .76	11	8.77 ± .67	5	−5.34	<.001
Foraging success (total mass gain; %)	14.09 ± 7.95	11	10.88 ± 7.95	5	−.74	.47
Time at sea (d)	10.93 ± 4.18	11	10.15 ± 2.27	5	−.39	.70
Daily distance covered (km/d)	514.33 ± 168.11	9	526.4 ± 52.9	5	.2	.85
Maximum foraging range (km)	1,257 ± 657.3	9	1,251.4 ± 311.39	5	−.02	.98

Note. *T*-tests were used to test for differences between sexes. All data are presented as means ± SD. N = sample size.

et al. 1992), starting from the most general model. This approach has been widely used in recent studies (Duriez et al. 2005; Grosbois and Thompson 2005; McDonough 2005). We calculated this second-order AICc using the formula

$$AICc = -2 \log \text{ likelihood} + 2K + 2K \frac{(K+1)}{(N-K-1)},$$

where N is the sample size and K is the number of parameters.

Values for difference in AICc values (ΔAICc) were computed by subtracting the minimum AICc from all candidate model AICc. Differences between AICc values for different models can be used to determine which one provides the most adequate description of the data on the basis of the fewest model parameters (Anderson et al. 2000). The model with the lowest AICc was considered the best fit that describes the relationship. ΔAICc values >2 are a good indicator that the model with the lowest AICc is preferable. ΔAICc values <2 indicate that models are fairly similar in their ability to describe the data, and the model including the fewest model parameters was then selected (Burnham and Anderson 2002).

We faced multicollinearity problems in our analyses because some of our explanatory variables were correlated (i.e., pretrip CORT level and foraging success were correlated with date). As suggested by Graham (2003), we assumed that one variable was functionally more important than the other to solve this problem. Thus, we assigned the more important variable priority over the shared contribution and ignored the shared contribution when analyzing the less important variable (Graham 2003). This was done by regressing the less important variable against the other and replacing the less important variable with the residuals from the regression (Graham 2003). Because explanatory variables are no longer statistically collinear, our models were unbiased (Graham 2003). Moreover, this method avoids the loss of explanatory power of shared contributions. As suggested by Graham (2003), we also based the priority on previously collected data and results. First, because CORT is

known to vary with food availability (Kitaysky et al. 1999), it is more relevant to test an effect of foraging success than an effect of date to explain posttrip CORT levels, and we therefore replaced the date variable with the residuals from the regression between date and foraging success in the starting model explaining posttrip CORT levels. Second, because subcutaneous implants of CORT are known to facilitate locomotor and foraging activity in vertebrates (review in Wingfield et al. 1998), it is more relevant to test an effect of pretrip CORT levels than an effect of date to explain components of foraging behavior. Before any analysis, we checked that these components of foraging behavior were unrelated to date of sampling by using linear regressions. We therefore replaced the date variable with the residuals from the regression between date and pretrip CORT levels in the starting model explaining components of foraging behavior.

Results

Correlates of CORT Levels

Plasma pretrip or posttrip CORT levels did not differ between sexes (Table 2). Plasma pretrip CORT levels decreased with sampling date (linear regression; before: $F_{1,14} = 9.09$, $P = 0.009$, $r^2 = 0.39$). The same trend was observed for plasma posttrip CORT (linear regression; after: $F_{1,9} = 3.85$, $P = 0.08$, $r^2 = 0.3$). There was no significant relationship between standardized pretrip body mass and plasma pretrip CORT level (linear regression; $F_{1,14} = 0.003$, $P = 0.96$). In contrast, standardized posttrip body mass and plasma posttrip CORT level were negatively correlated (linear regression; $F_{1,9} = 7.45$, $P = 0.02$, $r^2 = 0.45$).

At the individual level, plasma CORT levels significantly decreased after a foraging trip (paired t-test, $N = 11$, $t = 4.81$, $P = 0.001$; Fig. 1). Foraging success (as measured by mass gains) did not differ between males and females (Table 2) but slightly improved overall with sampling date over the course of the study (linear regression, $F_{1,14} = 3.72$, $P = 0.074$, $r^2 = $
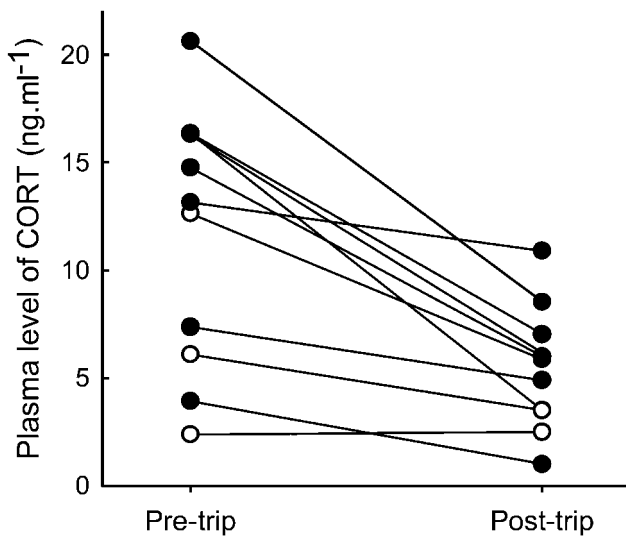
Figure 1. Individual changes in pretrip and posttrip CORT levels in wandering albatrosses. Open symbols denote females, and filled symbols denote males.

0.21). To explain posttrip CORT levels, the model selection demonstrated no effect of residuals from the regression between date and foraging success but a strong negative influence of foraging success on posttrip CORT levels (see Table 3 for parameter estimates; $\bar{r}^2 = 0.504$; Fig. 2).

Pretrip Corticosterone Levels and Subsequent Foraging Behavior

There was no difference between sexes for time at sea, daily distance traveled, or maximum range (Table 2). Moreover, none of these foraging variables varied significantly with date ($P > 0.05$ for all the regressions and for the GLM, which include date and time at sea variables to explain maximum range).

First, we found by using the step-down model selection that no explanatory variables explained time at sea. The reduced model, which contained only the intercept term, was preferred over the more complex model. Therefore, pretrip CORT levels, standardized pretrip body mass, and residuals from the regression between date and pretrip CORT levels were not linked to time at sea (Fig. 3a).

Second, daily distance traveled was not influenced by standardized pretrip body mass or by residuals from the regression between date and pretrip CORT levels (Table 3). However, the model selection demonstrated a positive effect of pretrip CORT levels on daily distance traveled (see Table 3 for parameter estimates; $\bar{r}^2 = 0.303$; Fig. 3b).

Third, there was strong evidence for a positive effect of both time at sea and pretrip CORT levels on maximum range from the colony (see Table 3 for parameter estimates; $\bar{r}^2 = 0.525$; Fig. 3c). However, maximum range was not influenced by the residuals from the regression between sampling date and pretrip

CORT levels or by standardized pretrip body mass (Table 3). Because this relationship could have resulted from statistical outliers, we examined the influence of each observation on the estimated regression coefficients using Cook's distance. No data points were found to be potential outliers (all Cook's distances were <1.0; Cook 1977).

Discussion

Corticosterone, Body Mass, and Foraging Success

In smaller albatross species, such as gray-headed (*Thalassarche chrysostoma*) and black-browed (*Thalassarche melanophris*) albatrosses, the decline in adult body condition at the end of a long incubation shift is mirrored by a rise in baseline CORT levels (Hector and Harvey 1986). However, a decline in adult body condition does not result in a rise in CORT levels in the wandering albatross because baseline CORT shows no clear pattern during a prolonged incubation shift (17 d; Hector and Harvey 1986). Accordingly, we found no relationship between baseline CORT levels and body mass at the end of the incubation shift, that is, pretrip CORT and pretrip body mass. In our study, we did not measure pectoral muscle depots or plasma metabolites such as uric acid to test whether protein catabolism (phase III; Cherel et al. 1988) has occurred in some birds measured at the end of an incubation shift (pretrip body mass). Because baseline CORT levels and body mass are negatively correlated when birds are depleting their protein reserves (Cherel et al. 1988; Romero and Wikelski 2001), the absence of such a relationship in our study suggests that wandering albatrosses were relieved of the fast before protein reserves were seriously depleted (Le Ninan et al. 1988). Wandering albatrosses have a wide safety margin of energy reserves and are able to buffer the costs of fasting for several weeks without neglecting their egg (Weimerskirch 1995, 1999). Indeed, in our study, average pretrip body mass (Table 2) was above body mass recorded for deserting wandering albatrosses (8.4 and 5.27 kg for males and females; Weimerskirch 1995).

Because baseline CORT levels are known to be negatively correlated with food abundance in seabirds (Kitaysky et al. 1999), we predicted that foraging success (total mass gain over a foraging trip) negatively affects plasma levels of posttrip CORT. According to this prediction, we found that individual CORT levels decreased during a foraging trip and that posttrip CORT levels were negatively correlated with foraging success. Thus, we showed for the first time in a free-living species that CORT levels can be significantly influenced by the ability of an individual to acquire food from its environment (foraging success). The pattern of CORT changes we described for wandering albatrosses is similar to that found in several mammals, including humans: baseline CORT increases slightly right before feeding (suggesting a shift in food anticipatory activity; Woodley et al. 2003), and food intake is associated with a decrease in baseline CORT (Krieger 1974; Mistlberger 1994; Hau and

Table 3: Model selection using Akaike's Information Criterion (AICc) and a step-down approach starting from the most general model

Dependent Variable and Models	K	Log Likelihood	AICc	ΔAICc	Selected Model	Parameter	Estimate ± SE	χ^2	P
Posttrip CORT:									
Foraging success, res1	3	−23.11	54.62	3.11	Foraging success	Intercept	8.78 ± 1.19	54.7	<.001
Foraging success	**2**	**−23.21**	**51.51**	**0**	Foraging success	Foraging success (%)	−.30 ± .09	11.2	<.001
Intercept	1	−27.07	56.47	4.96					
Daily distance traveled:									
Pretrip CORT, pretrip mass, res2	4	−83.70	179.84	3.71	Pretrip CORT	Intercept	415.20 ± 51.05	66.2	<.001
Pretrip CORT, pretrip mass	3	−84.06	176.52	.39	Pretrip CORT	Pretrip CORT (ng/mL)	11.79 ± 4.78	6.09	.014
Pretrip CORT	**2**	**−85.52**	**176.13**	**0**					
Intercept	1	−88.05	178.43	2.30					
Maximum range:									
Time, pretrip CORT, pretrip mass, res2	5	−101.41	220.32	7.30	Time, pretrip CORT	Intercept	−232.46 ± 397.46	.34	.559
Time, pretrip CORT, pretrip mass	4	−101.83	216.10	3.08	Time, pretrip CORT	Time at sea (d)	96.19 ± 29.04	10.20	.001
Time, pretrip CORT	**3**	**−102.31**	**213.02**	**0**	Time, pretrip CORT	Pretrip CORT (ng/mL)	54.45 ± 17.05	10.97	.001
Time	2	−106.14	217.37	4.35					
Pretrip CORT	2	−106.36	217.81	4.79					

Note. Model explains posttrip corticosterone (CORT) level (baseline CORT level measured after a foraging trip; $N = 11$), daily distance traveled ($N = 14$), and maximum range ($N = 14$). Generalized linear models with normal distribution and identity link were used to test for variable effect. K indicates the number of parameters. Foraging success, pretrip CORT, and pretrip mass indicate, respectively, mass gain in percent during the foraging trip, baseline corticosterone level, and standardized body mass measured before a foraging trip; res1 and res2 indicate, respectively, the residuals from the regression between date of sampling and (1) foraging success and (2) pretrip CORT levels. The best model is in bold. The right part of the table includes the parameter estimates for the selected model.
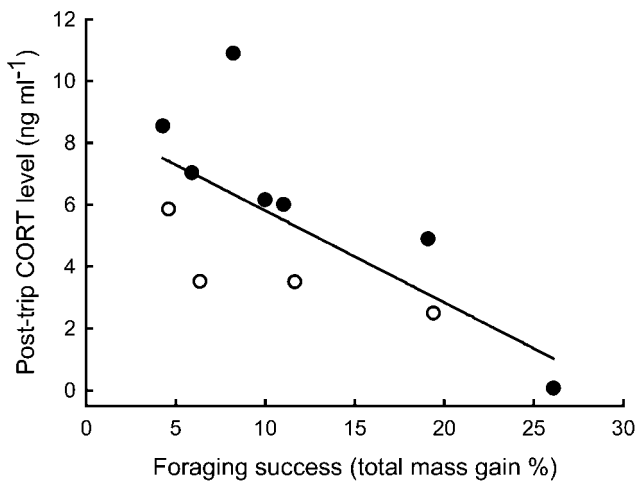
Figure 2. Relationship between plasma levels of posttrip CORT and foraging success (total mass gain as percent of body mass) in wandering albatrosses ($N = 11$). Open symbols denote females, and filled symbols denote males.

Gwinner 1996). Hence, the more energy an albatross acquired, the more pronounced the decline in CORT levels. The functional effect of food intake on CORT levels (Dallman et al. 1993) could then explain the decrease in baseline CORT levels during foraging activity, as documented for marine iguanas *Amblyrhynchus cristatus* (Woodley et al. 2003).

Corticosterone and Foraging Behavior

In this study, CORT levels, foraging success, and behavior were similar between males and females, illustrating a similar foraging effort between sexes in wandering albatrosses during the incubation period (Weimerskirch 1995). Because CORT might facilitate locomotor activity (review in Wingfield et al. 1998), we predicted that pretrip CORT levels should be positively correlated with daily distance traveled and maximum range. Despite the lack of an effect of CORT on time at sea, we found that pretrip CORT levels were positively correlated with daily distance traveled. Because prolonged time at sea of course allows birds to move farther, we found a positive effect of time at sea on maximum range. More importantly, we found a positive effect of pretrip CORT on maximum range. These findings provide strong correlative evidences that elevated pretrip CORT facilitates increased foraging-related locomotor activity (daily distance traveled), which allows albatrosses to move farther during a foraging trip (maximum range).

First, relationships between pretrip CORT levels and daily distance traveled or maximum range were independent of pretrip body mass, suggesting that slight variations in pretrip CORT levels rather than pretrip body mass might facilitate locomotor activity in the wandering albatross during the incubation period. This interpretation is consistent with several

studies that have demonstrated the influence of CORT on locomotor behaviors (review in Wingfield et al. 1998). For instance, Lõhmus et al. (2003) showed that CORT is associated with the expression of migratory activity and orientation in
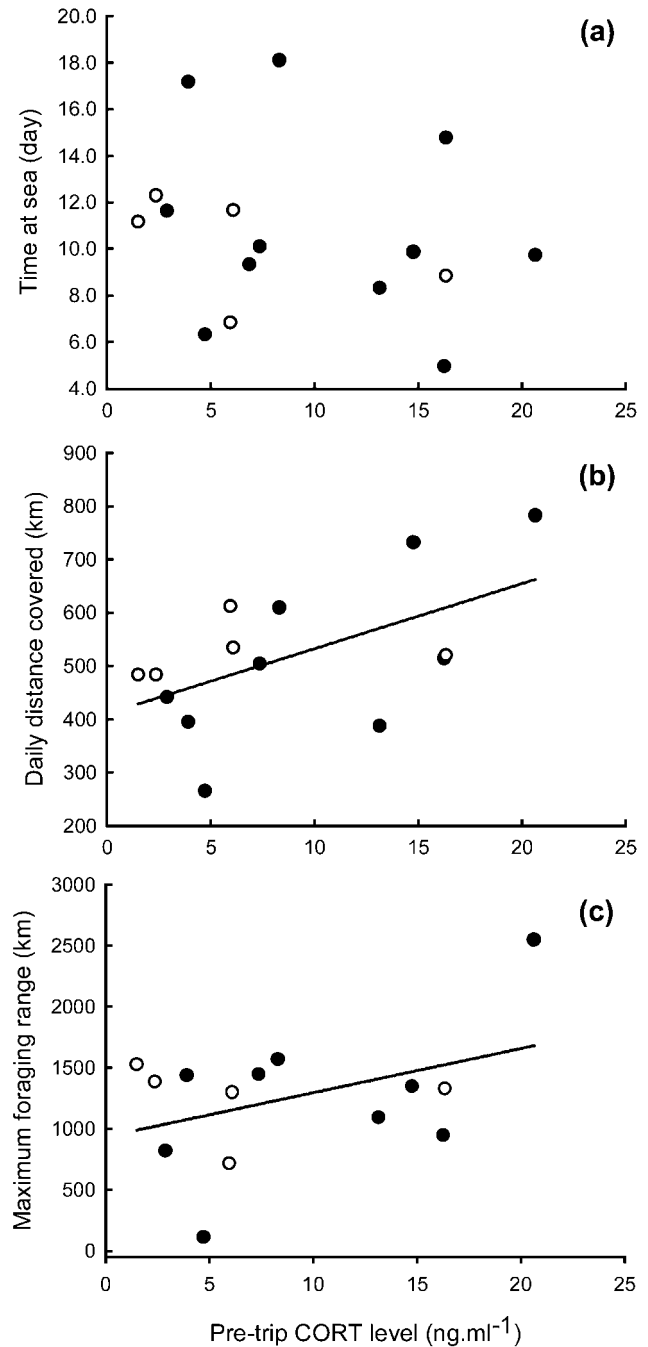

Figure 3. Relationship between time at sea (a; $N = 16$), daily distance traveled (b; $N = 14$), and maximum range of the foraging trip (c; $N = 14$) and pretrip CORT levels of wandering albatrosses. Open symbols denote females, and filled symbols denote males.

red-eyed vireos *Vireo olivaceus*, and Landys-Ciannelli et al. (2002) showed that CORT level increases in bar-tailed godwit *Limosa lapponica* in preparation for migratory flight. CORT is also implicated in food-searching activity: white-crowned sparrows *Zonotrichia leucophrys gambelii* implanted with exogenous CORT increased their activity range during good weather (Breuner and Hahn 2003). Finally, Astheimer et al. (1992) demonstrated that exogenous CORT induces a seven- to ninefold increase in activity in food-stressed captive white-crowned sparrows. A similar mechanism might occur in albatrosses: birds departing to the sea with elevated pretrip CORT levels travel farther from the colony and fly more distance per day, which probably increases their probability of encountering a prey patch (Weimerskirch et al. 1997). If CORT levels can be influenced by foraging success and can act on locomotor activity, this hormone might then represent the functional mechanism linking foraging decisions (daily distance traveled and maximum foraging range) to foraging condition encountered (food availability) in the wandering albatross.

However, because our study is correlative, the relationship between pretrip CORT and foraging behavior should be interpreted cautiously. For example, such a result can also be viewed as an effect of individual foraging ability and quality. Elevated pretrip CORT levels might result from a lower individual foraging ability during the previous foraging trip. Because poor foragers may be less efficient at detecting prey or may have a lower access to resources than good foragers, they may have to forage farther from the colony to obtain food, therefore explaining the positive relationship between pretrip CORT levels, daily distance traveled, and maximum range. Such interpretation is not incompatible with a functional effect of pretrip CORT on foraging behavior (review in Wingfield et al. 1998), but the data presented here cannot disentangle the potential confounding effect of individual quality.

In this study, we showed for the first time that individual foraging success can explain variation in CORT levels in birds returning from a foraging trip. Because we examined how CORT levels fluctuate within a normal range compatible with reproduction, we were able to highlight the sensitivity of CORT levels to variation in energy intake. We found also that daily distance covered and maximum foraging range at sea were positively correlated with pretrip CORT levels. This suggests that a small variation in baseline pretrip CORT levels might facilitate foraging behavior. Because our study is correlative and limited to one species, the field is open to promising empirical and experimental research. The challenge for the future is to identify the functional relationship linking foraging conditions, CORT levels, and foraging decisions (Weimerskirch 1999). Such a promising research field would definitely benefit from experimental manipulations of CORT levels using subcutaneous implants (Astheimer et al. 1992; Breuner and Hahn 2003; Kitaysky et al. 2003) associated with detailed flight and behavioral

data provided by recent advancements in miniaturized GPS systems (Weimerskirch et al. 2002).

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