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Ecophysiological response to an experimental increase of wing loading in a pelagic seabird

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Abstract

The knowledge of ecophysiological responses in relation to foraging effort is crucial to understanding feeding strategies, survival and reproductive trade-offs, as well as to obtain reliable indicators of an excessive workload. We present an integrative approach that examines a suite of ecophysiological parameters in relation to increased workload. We experimentally increased wing loading of 10 Cory's shearwaters *Calonectris diomedea*, a medium-sized pelagic seabird, by adding 45 g extra weight and compared their ecophysiological responses with 10 control birds. Among all the parameters analysed, the only significant response to overloading was a longer foraging trip, a lower rate of mass gain whilst at sea, and an increase in plasma levels of creatine kinase and lactate dehydrogenase activity indicating muscular damage. The analyses on these muscular enzymes open new opportunities to measure the impact of instruments on birds and to understand physiological responses in relation to foraging activity.

Keywords: Foraging activity; Nutritional state; Physiological stress; Stable isotopes

1. Introduction

Foraging activity is a major component of reproductive effort in most of a vertebrate's life. Foraging implies an effort which influences behaviour, reproductive success and physiological condition. In the last decade, foraging ecology has been mainly studied by deploying a wide array of instruments, particularly in seabirds and mammals, despite the potential changes in behaviour resulting from the additional weight and increased drag associated with these external devices (Gentry and Kooyman, 1986; Gaunt and Oring, 1998; Murray and Fuller, 2000; Phillips et al., 2003). Nevertheless, what initially arose as one of the main problems of instrumenting animals has become an experimental manipulations of foraging effort, bringing insights into understanding the impact of foraging costs on flying and diving performance, rate of energy delivery or offspring condition (*i.e.* Boyd et al., 1997; Weimerskirch et al., 2000; Paredes et al., 2005). To examine responses of an increase of foraging effort in free-living animals, researchers have traditionally measured changes in body mass and trip duration, whereas physiological responses have hitherto received little attention (Navarro and González-Solís, 2007). Such responses are crucial to understanding foraging strategies and survival and reproductive trade-offs, as well as to obtain reliable indicators of an excessive workload.

Foraging effort in birds is closely related to the flying exercise. Physiological responses to exercise have been widely studied in sports sciences and in domestic animals (*i.e.* Hinchcliff et al., 1998; Clarkson and Hubal, 2002). While energetic aspects of bird flight are relatively well known (Whittow, 2000), comprehensive studies on ecophysiological responses to an endurance flight are still scarce. Moreover, most existing studies focus on specific parameters and on migration rather than on foraging activity (Guglielmo et al., 2001). In endurance exercise, such as long distance flights performed by many bird species, muscles are damaged, showing an ultrastructural disruption and an increase in levels of specific-muscle enzymes, such as creatine kinase and

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lactate dehydrogenase (Fudge, 2000). Muscular damage can entail difficulties in obtaining enough quantity or good quality food, depleting nutritional condition and consequently it could affect some components of the immune system, such as the T-cell mediated immune response (Field, 2000; Alonso-Álvarez and Tella, 2001). Moreover, effort can provoke a stressful situation by increasing rapidly the levels of corticosterone hormone in plasma (review in Wingfield and Sapolsky, 2003). This hormone has also been directly involved in the regulation of foraging behaviour (Kitaysky et al., 2001; Angelier et al., 2007). In addition, foraging costs can influence diet choice and physiological state, modifying stable isotope signatures of C and N in plasma (Cherel et al., 2005), plasma biochemistry (Jenni-Eiermann and Jenni, 1998), and haematological parameters (Jenni et al., 2006).

Petrels are particularly appropriate to study ecophysiological responses to foraging effort because most species regularly perform sustained flights requiring a great endurance in muscular activity: they engage in long distance trips during several days or even weeks often covering thousands of kilometres (Brooke, 2004; González-Solís et al., 2007). Moreover, the large size of many petrel species allows the extraction of enough blood volume to perform a variety of haematological and biochemical analyses with ecophysiological interest. Here, we present a comprehensive approach on the ecophysiological responses to a workload increase, as indicated by changes in nutritional condition (plasma metabolites and body mass), oxygen carrying capacity (hematology), food resources exploitation (stable isotopes of N and C), muscle damage (creatine kinase and lactate dehydrogenase), immune system state (PHA assay) and physiological stress (corticosterone hormone). For this purpose, we experimentally increased wing loading with an extra weight during one foraging trip of 10 Cory's shearwaters, and compared their ecophysiological responses with 10 control birds.

2. Materials and methods

2.1. Model species

The Cory's shearwater is a colonial pelagic Procellariiform breeding on the northeast Atlantic and Mediterranean islands. Birds nest in rock crevices and burrows under rock or soil. The species shows a high reproductive investment (8 months), long incubation (54 days) and chick-rearing (90 days) periods and a life span of over 30 years. The species show long and slender wings adapted to combine gliding and active flight (Rosén and Hedenström, 2001). Incubation duties are shared by both sexes and when one partner is incubating the other one is foraging (see Thibault et al., 1997 for more details), mainly on areas located hundreds of kilometres from their breeding site (Mougin and Jouanin, 1997; Navarro and González-Solís, 2007).

2.2. Experimental procedure

We conducted the field experiment in Gran Canaria (15°47′ 18″ N; 27°50′41″ E, Canary Islands, Spain) during the incubation period of 2005 (May–July) at a breeding colony of about 150 pairs of Cory's Shearwaters that we were studying since 2002. Among all breeding pairs, we selected 20 females and randomly assigned half of them to the control group and the other half to the experimental group using a random number function (SPSS 15.0, 2006). We monitored the incubation routine (duration of incubation shifts and foraging trips) since the egg-laying (see Fig. 1). We carried out the experiment only on females to avoid potential sex related variability of the response. At the end of one foraging trip (referred as the first foraging trip, Fig. 1) we sampled 2 mL of blood and weighed the 20 females. Among them, the 10 experimental females were overloaded with 45 g of extra mass placed on the right leg using a plastic ring. This extra mass increased about 6% the wing loading (weight divided by wing area) of female Cory's shearwaters (body mass = 0.716 ± 0.05 kg, wing area = 0.13 ± 0.01 m^2, n = 44, authors unpublished data, see Pennycuick, 1989). Afterwards, we continued monitoring incubation routine since each bird returned from the subsequent foraging trip (referred as second foraging trip, see Fig. 1). At the end of the second trip, we sampled again 2 mL of blood, weighed all birds and removed the extra mass of overloaded females. To minimize potential interferences of circadian-rhythms on the variability of blood chemistry values, birds were sampled between 9:00 and 11:00 (GMT). Similarly, to minimize potential effect of manipulation on corticosterone and muscular

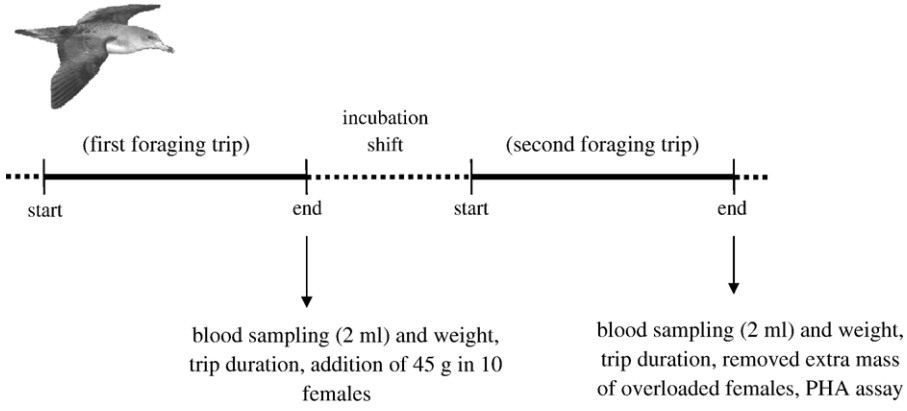

Fig. 1. Sampling protocol conducted throughout the experimental study.

enzyme levels we caught birds by hand from their burrows and took blood samples within the following 2 min (Romero and Reed, 2005). The 2 mL of blood extracted at the end of the each foraging trip was transferred to a vial containing lithium heparin for subsequent chemical analysis and plasma isotopic signatures.

All females (control and experimental) were tested for cell mediated immune response (CMI) by injecting 0.05 mL of 2 $mg \cdot mL^{-1}$ phytoaemagglutinin (PHA, Sigma) in phosphate buffered saline into a marked site on the right external foot web at the end of the second foraging trip (Fig. 1). The PHA assay test provides a measure of the proliferative response of circulating T lymphocytes to an injected mitogen. The main cellular response, as the amount of swelling 24 h after the injection, consists of a prominent perivascular accumulation of T lymphocytes followed by macrophage infiltration (Smits et al., 1999). The thickness of the foot web was measured with a digital micrometer (Mitutoyo, ±0.001 mm) at the injection site just prior to and 24 h after injection. Thickness measurements were repeated three times to minimize measurement error. CMI was calculated as the thickness increment between the injection time and 24 h later (Smits et al., 1999).

2.3. Laboratory analyses

Lithium heparinised blood was stored at 2–4 °C until haematological and biochemical analyses, which were conducted within 8 h of extraction. We determined haematocrit in a 70 μL capillary after centrifugation for 8 min at 12,000 rpm. Haemoglobin was measured photometrically using a spectrophotometer CLIMA 3.01 (RAL, Spain) after Drabkin's haemolysis using commercial kits (RAL, Spain).The remaining blood (1.9 mL) was centrifuged at 5500 rpm for 10 min and muscular-specific enzymes and nutritional metabolites were determined using a spectrophotometer and commercial kits (Clima 3.01; RAL, Spain). Creatine kinase, lactate dehydrogenase and urea concentrations in plasma were measured following UV-kinetic method (Thomas, 1998). Whereas the concentrations of triglyceride, cholesterol, total protein and uric acid in plasma were measured by the colorimetric method (Thomas, 1998). 0.7 mL of plasma was frozen at −22 °C for corticosterone hormone and stable isotopes analyses ($\delta^{15}N$ and $\delta^{13}C$ signatures). Plasma concentration of total baseline corticosterone was determined at the CEBC by radioimmunoassay following procedures previously described (Lormée et al., 2003). To analyse stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) plasma was dried at 60 °C for 24 h to remove ethanol and 0.4 mg of homogenized plasma was weighed to the nearest μg and placed into a Sn capsule. The samples were oxidized with CuO and CO_3O_4/Ag at about 900 °C in a Flash EA 1112 Elemental Analyser coupled to a pyrolyzer TC-EA and a breath bench, through an interface Conflo III Finnigan MAT. NO_2 was reduced with Cu at 680 °C. Combustion products N_2 and CO_2 were dried using MgClO4 and transported to a Delta C Finnigan MAT mass spectrometer (Isotopic ratio mass spectrometry, Serveis Científico-Tècnics of University of Barcelona, Spain) which applies international standards, generally run for each of 12 samples; IAEA CH_7 (87% of C), IAEA CH_6 (42% of C) and USGS 24 (100% of C) for ^{13}C and IAEA N1 and IAEA N2 (with 21% of N) and IAEA NO_3 (13.8% of N) for ^{15}N.

Table 1
Functional interpretation, initial value and percentage change (% Δ) for foraging trip duration, muscular enzymes, physiological state, hematology, corticosterone and stable isotopes in control and overloaded (45 g extra weight) females

Parameters	Functional interpretation	Initial	Control (% Δ)	Overloaded (% Δ)	*F*	*P*
Foraging trip duration	Changes in foraging costs[a]	9.65±2.18 (days)	−1.2±22.4	37.5±26.8	12.3	<0.001
Muscular enzymes activity						
Creatine kinase	Muscle damage[b]	51.11±37.98 (U/L)	165.8±189.8	610.6±475.4	7.55	0.01
Lactate dehydrogenase	Muscle damage[b]	67.85±34.25 (U/L)	−12.6±26.7	25.5±50.6	4.44	0.04
Physiological state						
Total protein	Protein turnover[c]	2.83±0.44 (g/dL)	−9.7±7.3	−5.6±15.9	0.54	0.47
Triglyceride	Fat metabolism[c]	54.52±14.41 (mg/dL)	−0.4±22.8	1.4±24.7	0.03	0.86
Cholesterol	Fat metabolism[c]	149.45±31.76 (mg/dL)	3.8±26.4	10.1±27.6	0.26	0.16
Uric acid	Protein catabolism[c]	3.87±2.81 (mg/dL)	26.4±191.9	−17.6±66.9	0.47	0.50
Urea	Protein catabolism[c]	10.51±4.82 (mg/dL)	−17.5±23.2	−13.7±45.1	0.06	0.81
Body mass	Body condition[d]	803.35±41.43 (g)	0.4±3.9	−7.7±6.9	8.67	<0.01
Hematology						
Hematocrit	Oxygen carrying capacity[e]	41.81±2.87 (%)	−2.7±5.1	1.5±11.9	1.07	0.31
Haemoglobin	Oxygen carrying capacity[e]	17.23±9.67 (g/dL)	−3.8±7.3	−0.3±7.9	1.11	0.31
Stress hormone						
Corticosterone	Physiological stress[f]	31.07±2.45 (ng/mL)	79.88±101.59	56.83±86.93	0.29	0.59
Stable isotopes						
Plasma $\delta^{15}N$	Trophic level during last week of sampling[g]	12.48±0.24 (‰)	1.37±2.91	1.97±2.96	0.21	0.65
Plasma $\delta^{13}C$	Feeding grounds during last week of sampling[g]	−16.91±0.79 (‰)	−0.79±6.23	−3.16±5.18	0.84	0.37
Cell mediated immunity	Immune system affect[h]		0.38±0.10	0.48±0.13	−1.66	0.12

Cell immunity mediated response for the 10 control and 10 overloaded females is also indicated.
Individual percentage variation = 100 × [(value at the end of second foraging trip − value at the end of first foraging trip) / value at the end of first foraging trip]. Initial values refer to the 20 females. Values are means ± standard deviation.
[a]Boyd et al. (1997); [b]Fudge (2000); [c]Jenni-Eiermann and Jenni (1998); [d]Brown (1996); [e]Davey et al. (2000); [f]Wingfield and Sapolsky (2003); [g]Cherel et al. (2005); [h]Smits et al. (1999).

2.4. Statistical analyses

To study the overload effect of the increase in wing loading on muscular damage, nutritional condition, haematological parameters, trip duration and diet, we calculated the percentage changes at the end of the second foraging trip with respect to the end of the first foraging trip of control and overloaded females. To evaluate the treatment effect on each percentage change we applied the ANOVA test, including treatment (control or handicapped) as fixed factors. We used an arcsine transformation to normalize percentage data before ANOVA test.

2.5. Ethical note

The experimental approach was conducted by permission from the Spanish Government. No female abandoned the nest during the experiment and all eggs hatched.

3. Results

Mean percentage variation of muscular enzymes (creatine kinase and lactate dehydrogenase), and trip duration were significantly greater for overloaded than for control females (Table 1; Fig. 2). Moreover, the percentage variation of the body mass increment was significantly lower for overloaded than for control females (Table 1). However, when adding the extra weight (45 g) to the body mass values of the overloaded birds, significant differences between control and overloaded birds did not hold (control = 0.68 ± 4.32%, overloaded = −2.08 ± 2.21, $t = 1.07$, $p = 0.31$). None of the variations in the nutritional metabolites, hematological, hormonal and stable isotopes signatures differed significantly between control and overloaded females (Table 1). Finally, cell mediated immune response did not differ between control and overloaded females (Table 1).

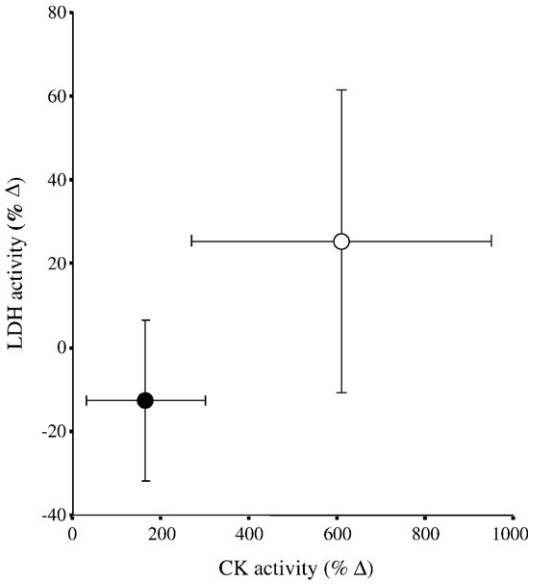

Fig. 2. Percentage variation (% Δ) of the creatine kinase (CK) and lactate dehydrogenase (LDH) activity for control (filled circle) and overloaded (open circle) Cory's shearwaters. Values are means and 95% confidence interval. See Table 1 for statistical tests.

4. Discussion

As expected, overloaded shearwaters substantially increased trip duration in response to the extra weight, as previously reported for many other seabird and pinniped species (Weimerskirch et al., 2000; Ballard et al., 2001; Taylor et al., 2001; Paredes et al., 2005). In response to the increase in wing loading, the fixed investment hypothesis predicts that long lived animals, such as shearwaters, should maintain their physiological state by increasing trip duration, thus transferring the extra costs to the partner or the offspring and minimizing the impact on their own survival (Tveraa et al., 1997; Weimerskirch et al., 2000; Navarro and González-Solís, 2007). In line with this prediction, most physiological parameters analysed did not differ between control and overloaded birds (Table 1). Plasma biochemical parameters related to the dynamics of protein turnover (total protein, uric acid and urea) and fat stores (triglycerides and cholesterol) showed similar values in both groups (Table 1). Overloaded birds may have experienced a decrease in the hematological values (Jenni et al., 2006), however in the present study hematological parameters did not differ between control and overloaded birds. Possibly these parameters are more sensitive to high rates of energy consumption by flapping flight rather than the gliding flight of shearwaters (Whittow, 2000). Similarly, we expected corticosterone hormones to rise in overloaded birds, since the concentration of this hormone usually increase in stressful situations (Wingfield and Sapolsky, 2003). However, both control and overloaded birds showed similar increments in corticosterone, suggesting the experimental increase in wing loading did not inflict a strong physiological stress. In line with these results, the immune system state measured by PHA assay (Smits et al., 1999) did not differ between control and overloaded birds. Furthermore, we did not find differences in the stable isotopes, suggesting that both groups fed on similar prey types (Forero and Hobson, 2003).

However, overloaded birds did not apparently recover body mass since they showed significantly lower increment in body mass than control birds (Table 1). This result was probably related to the incapacity of overloaded birds to gather enough quantity of food for covering the greater energy demands imposed by their greater wing loading (Freed, 1981). Nevertheless, when we added the extra weight (45 g) to the body mass values of overloaded birds the differences between control and overloaded birds disappeared (see results). This result could also suggest that overloaded birds reduced their body mass to compensate the greater wing loading imposed by the extra weight (Norberg, 1981).

Although most ecophysiological parameters did not differ, we found the activity of two muscular enzymes (creatine kinase and lactate dehydrogenase) showed a significant increase in overloaded compared to control birds (Fig. 2). In general, the increment in these enzymes reflects muscular damage in birds and mammals mainly related to intense and sustained locomotor

exercise (Noakes, 1987; Guglielmo et al., 2001; Smith et al., 2004). Therefore, the experiment induced muscular damage in overloaded birds probably resulting from an increase in foraging effort, as indirectly indicated by the increase in trip duration. Alternatively, since we added 45 g of extra mass on one leg, muscular damage may reflect a decompensation in the gravity centre associated to the asymmetric overload, which may have led to the overwork and damage of specific muscles. If the later is true, our results would call for caution in the deployment of devices on legs or on any other asymmetric position. While muscle damage can occur rapidly, in general the repair process can be prolonged (Clarkson et al., 1992; Clarkson and Sayers, 1999). Apparently muscular damage did not seriously affect the immediate physiological state of birds since the immune system, nutritional status and corticosterone were not altered. Long term effects were not controlled in this study, but in a previous experiment of an increase in flying effort in Cory's shearwater by clipping the tip of the flight feathers, levels in muscular enzymes and others physiological indicators were similar between control and handicapped birds over the incubation and chick-rearing periods (Navarro and González-Solís, 2007). This opposite result may be related to the capacity of birds to regulate body mass in a long term basis and compensate for the extra wing loading or, alternatively, to the symmetric approach of this experimental manipulation.

In summary, our study examined a broad array of ecophysiological responses to an experimental increase in wing loading. Among all the parameters analysed, we found a significant increment of creatine kinase and lactate dehydrogenase levels in plasma in the overloaded individuals. Thus, our results suggest that the increased plasma levels of muscular enzymes may be used as an indicator of an excessive or decompensate flying effort in birds. The analyses on these enzymes open new opportunities to measure the impact of tracking instruments on birds and to understand physiological responses in relation to foraging activity.

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