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ORIGINAL PAPER

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Blood chemistry in relation to nutrition and ectoparasite load in Wilson's storm-petrels *Oceanites oceanicus*

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Abstract Haematology and plasma biochemistry values are useful tools for ecological research, providing information on the physiological state and adaptation of individuals to their habitat, changes in nutritional state of birds, body condition, the level of parasite infestation, etc. We studied the effect of stress factors on haematological and plasma biochemistry values in adult and nestling Wilson's storm petrels *Oceanites oceanicus* (Aves, Procellariiformes). We measured packed cell volume, triglyceride levels, plasma protein levels, plasma hue and plasma corticosterone of nestlings and breeding adults at King George Island, South Shetland Islands. We used a snow storm as a natural experiment to test what effect starvation has on the stress response of nestlings. In particular, we predicted that: (1) plasma protein concentrations and plasma hue reflect ectoparasite load, (2) triglycerides and hue reflect the nutritional state, and (3) corticosterone levels increase with ectoparasite load and starvation. In line with our predictions, plasma triglycerides were higher in nestlings than adults, indicating a resorptive nutritional state in nestlings, during which dietary fat is deposited in adipose tissues. In adults, plasma triglycerides were positively correlated with body mass. Corticosterone levels increased in response to handling in adults, while we did not find a stress response in nestlings in good condition. However, nestlings sampled after their nests had been blocked by a snow storm showed a stress response in excess of that of adults. In nestlings sampled after the snow storm, corticosterone peak levels were positively correlated with the infestation intensity of the ectoparasite *Philoceanus robertsi* (Phthiraptera: Ischnocera), suggesting that the stress response is increased when more stressors act at the same time. In adults, plasma hue and proteins decreased with increasing ectoparasite load.

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Introduction

The usefulness of haematology and plasma biochemistry as veterinary tools for the diagnosis of disease and the monitoring of the condition of birds is widely recognized (e.g. Dein 1986). Lately, clinical screening procedures that are conventional in human and veterinary medicine have also been used to assess the condition of free-living animals (e.g. Alonso-Alvarez et al. 2003; Christe et al. 2002; Dawson and Bortolotti 1997a, 1997b; Gauthier-Clerc et al. 2003; Jenni-Eiermann and Jenni 1992; O'Reilly and Wingfield 2003).

The condition of free-living animals is determined by a number of factors, including their nutritional state, the prevalence of parasites and the presence of stressors, such as extreme climatic conditions or reproductive effort. These factors are interrelated as, for example, birds in poorer nutritional condition may be more likely to be parasitized (e.g. Shutler et al. 1999). Because immune function interacts with the general health state of an organism and competes for the resources that can be allocated to other activities, studies of immunological ecology may offer a powerful tool for explaining how reproductive effort links to reproductive costs. Studies of the nutritional and immunological condition of free-living animals are also needed in state-dependent life-history models, in order to explain why individuals differ from each other with respect to their reproductive decisions.

An important issue regarding the application of haematology and plasma-biochemistry parameters to the study of natural animal populations is the choice of optimal research methodology. Different health-state indices measure different aspects of individual condition, and may also reflect acute or chronic health disorders. Moreover, there are potential sources of variation not directly related to the life-history components under examination, such as differences due to sex and age, awareness of which being of crucial importance for distinguishing between environmental noise and experimental effect.

Stressful events like limited food availability and infestation by parasites are regularly experienced by birds living in the wild. They demand changes in energy use in order to promote self maintenance. Corticosterone, the main glucocorticoid in birds, acts as a physiological signal in these situations when environmental conditions require modification of behaviours and metabolism. Long-lived birds often accumulate fat as energy reserves for self-maintenance during reproduction (Drent and Daan 1980). As fat reserves are depleted, birds rely more on catabolism of muscle protein (Cherel et al. 1988), which is stimulated by secretion of corticosterone. Plasma corticosterone levels have been found to correlate negatively with fat reserves, and are elevated in response to chronic starvation and low nutritional quality of food (Kitaysky et al. 1999a, 1999b; Nuñez-De la Mora et al. 1996; Wingfield et al. 1999). They are thus an alternative measure of body condition.

In the present study, we analyse haematology and plasma-biochemistry parameters in Wilson's storm petrels *Oceanites oceanicus*, the smallest endotherm animals breeding in the Antarctic. The Antarctic Ocean represents an extreme habitat with variable climatic conditions, and the breeding success of Wilson's storm petrels mainly depends on the abundance of zooplankton within the foraging range and on snow storms, which may cause nestling mortality when nest burrows become blocked and nestlings starve (Quillfeldt 2001).

Many seabirds, including Wilson's storm petrel, have been found free of blood parasites (Becker and Holloway 1968; Jovani et al. 2001; Merino and Minguez 1998; Merino et al. 1997). However, seabirds may have high levels of ectoparasites, and these have been shown to influence nestling growth in European storm petrels (Merino et al. 1999). The feather louse *Philoceanus robertsi* is found on adult and nestling Wilson's storm petrels (E. Mey, personal communication). This feather louse produces small holes in feathers, causing damage to the plumage (authors' observation). Although feather lice are generally thought to be relatively benign (e.g. Clayton and Tompkins 1995; Tompkins et al. 1996), they have been found to indirectly affect thermoregulation and feather quality of avian hosts (Booth et al. 1993; Kose and Møller 1999), as well as flight performance (Barbosa et al. 2002).

We studied the effect of stress factors on haematological and plasma-biochemistry values in adult and nestling Wilson's storm petrels *O. oceanicus* (Aves, Procellariiformes). We used a snow storm as a natural experiment to test what effect starvation has on the stress response of nestlings. In particular, we predicted that: (1) plasma protein concentrations and plasma hue reflect ectoparasite load, (2) triglycerides and hue reflect the nutritional state, and (3) corticosterone levels increase with ectoparasite load and starvation.

Materials and methods

Study site and study species

The study was carried out in the Tres Hermanos (Three Brothers Hill) colony on King George Island, South Shetland Islands (62°14′S, 58°40′W) in the maritime Antarctic from January to March 2000. Wilson's storm petrels are the smallest and one of the most abundant Antarctic seabird species. Their breeding biology was summarized by Beck and Brown (1972). They nest in colonies in scree slopes along ice-free Antarctic and sub-Antarctic coasts, where they lay a single egg in a natural cavity. Wilson's storm petrels exhibit intensive biparental care. Incubation and nestling feeding are shared between the sexes. The nestlings remain in the nest for about 60 days and are fed during brief nightly visits.

Study methods

Nests were inspected routinely to determine hatching success and collect data on nestling growth. Adults were captured by hand on their nests between 2000 and 2400 hours, when nestlings were 8 days old, then weighed, and their wings measured with a stopped wing rule to the nearest millimetre. Blood samples (100–150 μl) were collected from the brachial vein immediately after capture (handling time 1–2 min), or at 45 min or 90 min after restraint in a cloth bag. Each adult ($n=84$) was only sampled once. The plasma of 46 adults was analysed for protein and triglyceride contents, and the plasma of 38 adults was used for the analysis of corticosterone.

Nestlings ($n=50$) were sampled at 38–53 days of age after capture by hand, between 1200 and 1700 hours. As in adults, blood samples were taken immediately after capture (handling time 1–2 min), or at 45 min or 90 min after restraint in a cloth bag. The plasma of 17 nestlings was analysed for protein and triglyceride contents, and the plasma of 33 nestlings was used for the analysis of corticosterone. In accordance with most stress protocols, we took baseline as well as peak samples of several nestlings. However, statistical analyses were performed on either baseline or peak values, and thus no pseudoreplication occurred. Three parameters of the nestlings and attending adults were recorded: (1) body mass, using a digital balance to the nearest 0.1 g; (2) wing length, the distance from the anterior surface of the radio carpal joint to the tip of the longest primary, to the nearest 1 mm; (3) the number of rectrices with feather-louse bite marks. The body mass of adults was not correlated with measures of body size; therefore we used body mass in the analyses without calculating a relative index.

In March 2000, a snow storm blocked all nest entrances in the colony, and a superficial ice cover of 3–5 cm rendered the nests completely inaccessible to the attending adults for several days. The event resulted in the death of 40% of the nestlings (Quillfeldt 2001). We took blood samples of 15 surviving nestlings for the analysis of corticosterone.

Haematological methods

Packed cell volume (PCV) was measured with digital callipers to the nearest 0.1 mm after 10 min of centrifugation of heparinized capillary tubes at 10,000 rpm. After determination of haematocrit, plasma was separated from blood cells and stored at −20°C until analysed.

Total plasma protein and triglyceride concentrations were determined using standard spectrophotometric test combinations modified for small amounts of plasma (protein: 5 μl plasma per determination, procedure no. 610, Sigma Diagnostics; triglycerides: 3 μl plasma per determination, procedure no. 541, Sigma Diagnostics).

Plasma hue was scored on a scale of 1–4, against colour chips of Baumanns Farbtonkarte, where 1 (citrin) was closer to yellow and 4 (orange) was closer to red. To test repeatability of hue scores, 32 samples were taken with 2 separate capillaries, and stored and scored separately: 26 (81%) were scored identical (same hue value), while 6 (19%) were scored 1 point different. No samples were scored more than one point different.

We used 2 μl plasma without extraction, and an enzyme immunoassay (EIA) for corticosterone (Palme and Möstl 1997). Due to the small sample volume, our measurement limit was above 5 ng/ml. All values that could not be determined because of a too-low concentration were thus set to 5 ng/ml.

Statistical analyses

Data were analysed using Sigma Stat 2.03 and SPSS 11.0. Parametric statistical procedures were used for comparison of condition indices, except when the assumption of normality of data was violated (in which case non-parametric tests were used). Throughout this study, all means are given ±SE. The significance level used is $P<0.05$. Note that sample sizes for different analyses varied, as not all measurements could be taken on all birds.

Results

Differences between nestlings and adults

Adults had higher PCV and lower triglyceride levels than nestlings (Table 1). The plasma protein concentration did not differ between nestlings and adults (Table 1). The reddest plasma hue (score 4) was absent in nestlings. However, the overall distribution of plasma hues did not differ between adults and nestlings. There was no measurable difference in baseline corticosterone levels between adults and nestlings (Table 1). Most adults and nestlings had baseline corticosterone levels below our limit of detection. In contrast, many adults had elevated corticosterone levels at 45 min after capture (Fig. 1), which decreased again after 90 min ($n=12$). Nestlings, which were accustomed to handling, did not show this increase (Table 1). While most adults (64%) had no rectrices with bite marks of feather lice, all nestlings had bite marks (Fig. 2). Nestlings had higher infestation intensities than adults (Fig. 2, Mann-Whitney $U_{46,83}=4594.5$, $P=<0.001$).

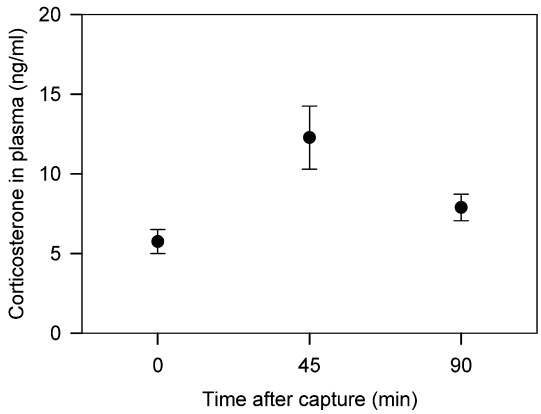


Fig. 1 Variation of plasma corticosterone in response to handling of adult Wilson's storm petrels at King George Island, breeding season 1999–2000. *Error bars* show mean and standard error

Adults—differences between sexes and influence of body mass and ectoparasites

We did not detect any difference in blood parameters between male and female Wilson's storm petrels (Table 2). The concentration of triglycerides was correlated with body mass ($R=0.363$, $n=46$, $P=0.015$, Fig. 3), but not with ectoparasite load (Spearmann $R=0.019$, $n=43$, $P=0.905$). Two of the haematological parameters (plasma proteins and hue) were correlated with the number of rectrices with feather-louse bite marks, a measure of parasite infestation intensity (Fig. 4, see legend for statistics). We found that PCV was not correlated to either body mass ($R=-0.109$, $n=82$, $P=0.329$) or ectoparasite load (Spearmann

Table 1 Natural variation of haematological parameters of nestlings and adults of Wilson's storm petrels at King George Island, breeding season 1999–2000

	Nestlings			Adults			Test
	Mean±SE	Range	*n*	Mean±SE	Range	*n*	
Packed red blood cell vol. (%)	39.2±4.7	30–49	17	50.8±0.4	44–56	46	Mann-Whitney $U=167.5$, $P<0.001$
Plasma proteins (g/dl)	2.6±0.1	1.7–3.6	17	2.7±0.1	1.8–3.7	46	$t=0.41$, *df* 61, $P=0.683$
Plasma triglycerids (mg/dl)	167.5±10.4	99.8–247.3	17	94.0±5.0	31.0–168.2	46	$t=7.06$, *df* 61, $P<0.001$
Plasma corticosterone (ng/ml) at 0 min (baseline value)	5.3±0.2	<5.0–9.1	26	5.8±0.8	<5.0–10.3	7	Mann-Whitney $U=126.0$, $P=0.772$
Plasma corticosterone (ng/ml) at 45 min (peak value)	5.2±0.2	<5.0–9.1	19	12.3±2.0	<5.0–35.8	23	Mann-Whitney $U=302.0$, $P=0.007$

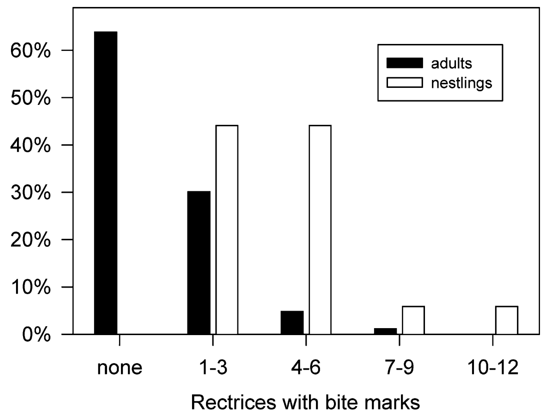


Fig. 2 Distribution of infestation intensity of feather lice *Philoceanus robertsi* (Phthiraptera: Ischnocera) in adult and nestling Wilson's storm petrels at King George Island, breeding season 1999–2000

$R = -0.039$, $n = 78$, $P = 0.736$). None of the haematological parameters were correlated with the wing length, a measure of body size.

Nestlings—influence of age and body mass

PCV in nestlings increased linearly with age (linear regression, $R = 0.50$, $F = 14.5$, $P < 0.001$, $n = 46$, snowstorm data excluded): PCV = 19.83 + 0.47*age(days). We thus tested for the relationship between PCV and body mass by partial correlation (controlling for age). There was no correlation between PCV and body mass ($R = -0.067$, $n = 46$, $P = 0.660$). The concentrations of plasma protein and triglycerides were not correlated with age (Pearson correlation for plasma protein $R = 0.102$, $n = 17$, $P = 0.696$, for plasma triglycerides $R = 0.160$, $n = 17$, $P = 0.539$) or with body mass (Pearson correlation for plasma protein $R = 0.221$, $n = 17$, $P = 0.393$, for plasma triglycerides $R = 0.289$, $n = 17$, $P = 0.260$). The concentrations of plasma protein and triglycerides were not correlated with ectoparasite load (Spearman correlation for plasma protein $R = -0.079$, $n = 17$, $P = 0.773$, for plasma triglycerides $R = -0.360$, $n = 17$, $P = 0.839$). Due to the properties of our analyses, we found not enough variation in baseline and peak corticosterone levels to determine variation with age, body mass or parasites.

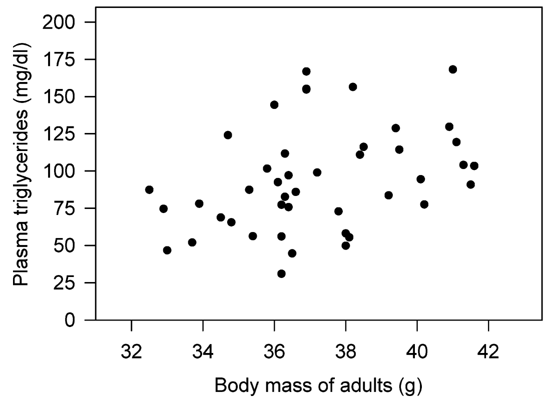


Fig. 3 Correlation between body mass and plasma triglyceride concentration in adult Wilson's storm petrels at King George Island, breeding season 1999–2000

Nestlings—influence of starvation

During a severe snow storm, nestlings were trapped in their blocked nests and adults had no access to the nests for several days. Nestlings lost an average body mass of 16 g (mass before snow storm 63.8 ± 11.9 g SE; after snow storm 48.2 ± 18.0 g SE). The PCV of nestlings was not influenced by the snow storm (General Linear Model, dependent: PCV, factor snowstorm: $F_{33,15} = 0.131$, $P = 0.718$, covariate age: $F = 32.1$, $P < 0.001$).

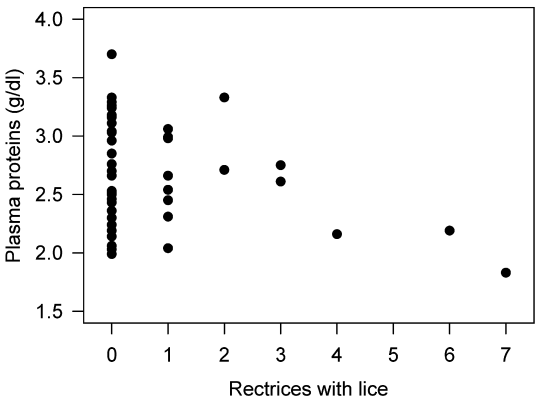
Corticosterone was increased after the snow storm (Fig. 5). The baseline corticosterone levels were increased to 10.7 ± 2.2 ng/ml (range < 5–39.8 ng/ml, compare Table 1, Wilcoxon Signed Rank Test for 12 pairs, $Z = 28.0$, $P = 0.016$). The peak corticosterone levels were increased to 17.2 ± 5.0 ng/ml (range < 5–64.3 ng/ml, compare Table 1, Mann-Whitney U-test, $U_{15,19} = 325.0$, $P = 0.030$). The measured baseline corticosterone levels were not sufficiently variable to determine variation with body mass or parasites. The peak corticosterone levels were not correlated to the body mass of nestlings after the snow storm ($R = 0.296$, $n = 15$, $P = 0.284$). The peak corticoste2rone levels were positively correlated with ectoparasite load (Spearman $R = 0.773$, $n = 12$, $P = 0.002$, Fig. 6).

Discussion

In line with our predictions, plasma triglycerides were higher in nestlings than adults, indicating a resorptive

Table 2 Natural variation of haematological parameters of male and female Wilson's storm petrels at King George Island, breeding season 1999–2000. Plasma corticosterone was measured at 45 min after initial capture

	Females			Males			Test
	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*	
Packed red blood cell vol. (%)	51.0 ± 0.6	44–56	23	50.7 ± 0.5	46–56	23	$t = 0.35$, *df* 44, $P = 0.732$
Plasma proteins (g/dl)	2.7 ± 0.1	1.8–3.6	23	2.7 ± 0.1	2.0–3.7	23	$t = 0.16$, *df* 44, $P = 0.873$
Plasma triglycerids (mg/dl)	92.3 ± 8.1	31.0–168.2	23	92.8 ± 6.2	46.8–155.2	23	$t = 0.24$, *df* 44, $P = 0.813$
Plasma corticosterone (ng/ml)	12.2 ± 2.6	< 5.0–26.0	12	12.4 ± 3.2	< 5.0–35.8	11	Mann-Whitney $U = 110.0$, $P = 0.766$



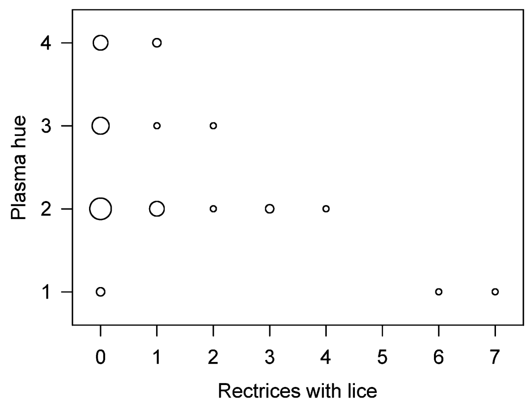


Fig. 4 Variation of plasma proteins and plasma hue with infestation intensity of feather lice *Philoceanus robertsi* (Phthiraptera: Ischnocera) in adult and nestling Wilson's storm petrels at King George Island, breeding season 1999–2000. The mean hue and the mean protein concentration decreased with lice load (Spearman $R = -0.982$, $n = 7$, $P < 0.001$ for hue; $R = -0.842$, $n = 7$, $P = 0.017$ for protein). Differences in the size of the *symbols* represent sample sizes

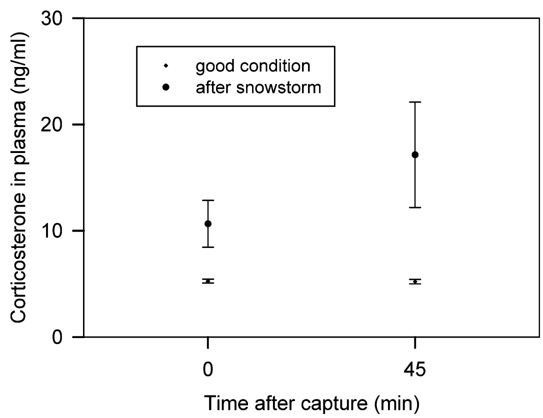


Fig. 5 Variation of plasma corticosterone in response to handling of nestling Wilson's storm petrels at King George Island, breeding season 1999–2000. *Small symbols* are shown for nestlings in good condition, while *large symbols* are shown for nestlings after several days of starvation, caused by a snow storm blocking nest entrances (*error bars* show mean and standard error)

nutritional state in nestlings, during which dietary fat is deposited in adipose tissues. In adults, plasma triglycerides were positively correlated with body mass. Corticosterone levels increased in response to handling in adults, while we did not find a stress response in nestlings in good condition. However, nestlings sampled after their nests had been blocked by a snow storm showed a stress response in excess of that of adults. In nestlings sampled after the snow storm, corticosterone peak levels were positively correlated with feather-louse infestation intensity, suggesting that the stress response is increased when more stressors act at the same time. In adults, plasma hue and proteins decreased with increasing ectoparasite load.

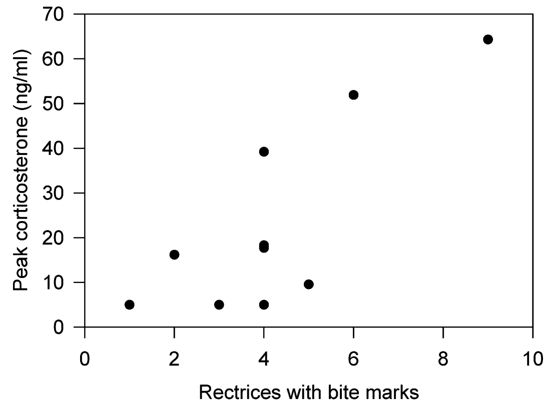


Fig. 6 Relationship between feather-lice infestation and plasma corticosterone in response to handling of nestling Wilson's storm petrels at King George Island, breeding season 1999–2000, after starvation caused by a snow storm

Packed cell volume

PCV (haematocrit) is a measure of red-blood-cell volume, showing variation with age, moulting, reproductive cycle, air temperature and species in birds (Dein 1986). Low values of haematocrit may indicate pathologies like anaemia, due to diseases and parasites (e.g. Averbeck 1992; Dein 1986; Hurtrez-Boussès et al. 1997), while high values might indicate elevated oxygen consumption accompanying an intense work load (Carpenter 1975; Saino et al. 1997a, 1997b).

We found that nestlings of 40 days of age had much lower PCV than adults. The only two species of Procellariiformes studied so far, to our knowledge, show a relatively delayed development of blood oxygen-carrying capacity compared with other birds. The long and slow nestling development of Procellariiform seabirds can be divided into three phases (e.g. Quillfeldt and Peter 2000): an initial phase immediately post-hatching with little mass gain, a phase of rapid, approximately linear, weight gain until reaching peak mass, and a period of mass recession until fledging. In Wilson's storm petrels (Kostelecka-Myrcha and Myrcha 1989) and short-tailed shearwaters *Puffinus tenuirostris* (Arnold et al. 1999), haematocrit was constant during the phase of rapid mass gain, but increased markedly after the attainment of peak mass, resulting in a total increase in blood oxygen-carrying capacity from hatching to fledging of about 70%. Fledgling short-tailed shearwaters reached about 81% of adult oxygen-carrying capacity (Arnold et al. 1999). Similar values were reported for chinstrap penguins (*Pygoscelis antarctica*) (Merino and Barbosa 1997), and the authors suggested that this may be due to low exercise and oxygen demands in nestlings as compared to more active adults. Similarly, in Wilson's storm petrels, the nestlings are confined to the nest crevices, while the adults carry out long provisioning trips.

We found that PCV was not correlated to either body mass or ectoparasite load. Similar to the present results, several studies have reported negative results of correlation of PCV with condition. Dawson and Bortolotti (1997a, 1997b) found that PCV was not indicative of nutritional status and condition in adult or juvenile American kestrels (*Falco sparverius*). Johnson et al. (1991) and O'Brien et al. (2001) found no effect of ectoparasitism on PCV of nestling house wrens (*Troglodytes aedon*). Moreno et al. (1998) reported that PCV was not different between early and late breeders in chinstrap penguins, although late breeders had poorer health (more leucocytes, lower T-cell-mediated immune response) than early breeders, and similarly, Gauthier-Clerc et al. (2003) found no effect of tick infestation on PCV in king penguins (*Aptenodytes patagonicus*). In contrast, in serin (*Serinus serinus*) nestlings, haematocrit values were positively correlated with food availability (Hoi-Leitner et al. 2001).

Plasma protein concentration and ectoparasite load

Total plasma protein content is considered to indicate nutritional state (e.g. Jenni-Eiermann and Jenni 1996; Ots et al. 1998). Moreover, low serum protein (<2.5 g/dl) may indicate chronic disease, stress or starvation, while high (>5 g/dl) values are found during acute infections (Lewandowski et al. 1986).

In line with Lewandowski's first suggestion (Lewandowski et al. 1986), we found that the mean plasma protein concentration was low in adult Wilson's storm petrels with high ectoparasite load (Fig. 4). However, a proportion of adults without lice bite marks also had low serum protein (<2.5 g/dl), indicating that feather lice are not the only factor determining plasma protein in the blood.

The plasma protein concentration did not differ between nestlings and adults (Table 1). It was not correlated to body mass. Similar to the present results, Dawson and Bortolotti (1997b, 1997c) did not find a relation between plasma proteins and condition in nestling and adult American kestrels.

Newman et al. (1997) found that 13 species of Alaskan seabirds had mean total protein concentrations between 3.2 and 4.9 g/dl. This is in agreement with other bird taxa (Dein 1986), and indicates that Wilson's storm petrels have a mean protein level lower than most species.

Plasma triglycerides and nutritional state

Higher levels of plasma triglycerides indicate a resorptive nutritional state, during which dietary fat is deposited in adipose tissues (e.g. Jenni-Eiermann and Jenni 1998). Low triglyceride levels, in contrast, are symptomatic of a post-resorptive fasting state during which triglycerides from adipose tissues are hydrolysed to free fatty acids and glycerol. Jenni and Schwilch (2002) found that the absolute mass was only marginally correlated with triglycerides in reed warblers, while the change in body mass was strongly correlated with triglycerides. They concluded that feeding leads to increase in body mass and increase in triglycerides. They could also show that the triglyceride concentration has a diurnal rhythm, depending on the rhythm of food intake.

We found that plasma triglycerides of Wilson's storm petrels were higher in nestlings than adults. This indicates that nestlings were in a more resorptive nutritional state, during which dietary fat is deposited in adipose tissues. Nestlings of tube-nosed seabirds accumulate large amounts of fat during their development. In adults, plasma triglycerides were positively correlated with body mass, indicating that heavy adults used a part of the ingested food to restore their own fat reserves. Thus, triglycerides may be a useful parameter when estimating how adults allocate resources. The absence of a relationship between triglycerides and body mass in nestlings may be explained by the good condition of all sampled nestlings, by the small sample size, or by the large daily fluctuations in body mass that the storm-petrel nestlings experience. We measured body mass on the day of sampling, but not the day before. Similar to Jenni and Schwilch (2002), the triglyceride level may depend on the change in body mass rather than on absolute mass.

In our sample of Wilson's storm petrels, adults had low values compared to those reported in the literature. Newman et al. (1997) compared 13 species of Alaskan seabirds, and found mean triglycerid concentrations between 144 and 472 mg/dl, compared with 94 mg/dl for adult Wilson's storm petrels. However, the birds Newman et al. (1997) used were of unknown breeding status, and probably included a substantial portion of young non-breeders. Future studies on triglyceride metabolism in seabirds should include diurnal and annual variation, and variation between age groups and breeding stages.

Plasma hue and feather-lice infestation

The hue of blood plasma reflects the amount and types of carotenoids carried in the blood. Because carotenoids have an antioxidant function and are required for carotenoid-specific immunomodulation (reviewed by Goodwin 1986), they may indicate the condition of individuals. For instance, it has been found in house finches (*Carpodacus mexicanus*) (Hill et al. 1994), that plasma hue is positively correlated to plumage coloration in adult males, and thus influences mate selection. A number of studies have demonstrated that plasma carotenoids in birds are reduced in response to bacterial infection (Koutsos et al. 2003), intestinal parasites (Allen 1992; Tyczkowski and Hamilton 1991) and viral infections (Page et al. 1982; Squibb et al. 1971).

In the present study, we found that adult Wilson's storm petrels with a high ectoparasite load had low plasma hues, indicating that infestation by ectoparasitic feather lice may also reduce plasma carotenoids. Alternatively, adults in poor immunological condition may be more susceptible to lice infestation. In adults with low feather-lice infestation, the whole range of plasma hues was represented, indicating that feather lice are not the only factor determining plasma carotenoids in the blood.

Corticosterone and starvation

Several studies of corticosterone levels in seabirds suggested that the plasma corticosterone levels are negatively correlated with body reserves, and are elevated in response to starvation (Kitaysky et al. 1999a, 1999b; Nuñez-De la Mora et al. 1996; Quillfeldt and Möstl 2003; Wingfield et al. 1999).

Our results are in line with previous studies on seabirds. Furthermore, the present results suggest that plasma corticosterone levels may be elevated in response to parasite infestation. Most adults and nestlings had baseline corticosterone levels below our limit of detection. Adults had elevated corticosterone levels at 45 min after capture (Fig. 1), while we did not find a stress response in nestlings in good condition (Table 1, Fig. 2). The data after a snow storm show that nestlings were capable of a strong stress response (Fig. 2), but this was not expressed while they were well fed and accustomed to daily handling. The stress response of nestlings sampled after their nests had been blocked by a snow storm was in excess of that of adults. In nestlings sampled after the snow storm, corticosterone peak levels were positively correlated with ectoparasite load, suggesting that the stress response is increased when more stressors act at the same time.

Quillfeldt and Möstl (2003) studied physiological stress in Wilson's storm petrels by measuring glucocorticoid metabolite levels in faeces and urine of nestlings and adults. Similar to the present study, glucocorticoid (GC) metabolite levels were elevated during starvation in nestlings. In contrast, adults did not show elevated GC levels, and even decreased GC in the course of the breeding season. Quillfeldt and Möstl (2003) found that nestlings had more than threefold mean excreted glucocorticoid levels compared to adults. This is in apparent contrast to the present results. However, most adults and nestlings had baseline plasma corticosterone levels below our limit of detection, such that all values below 5 ng/ml (which included 86% of adult samples and 92% of nestling samples) were overestimated, and the variation in these data was eliminated by our analyses. It would be desirable to study baseline plasma corticosterone levels using larger volumes of plasma, such that these low values could be measured more accurately, and their relationship with condition parameters could be established. Furthermore, as Quillfeldt and Möstl (2003) pointed out, there may be diurnal variation of circulating corticosterone, and samples should be taken at different times of the day in order to analyse this.

Conclusions and prospects

Former studies have shown that adult body mass cannot be used as a reliable measure of body condition in Wilson's storm petrels, because adults carry large food loads (up to 13 g, at a body weight of 38 g, Quillfeldt and Peter 2000). In the present analysis, we tested the role of haematological parameters in determining individual quality and condition of adult and nestling Wilson's storm petrels *O. oceanicus*. We found that PCV had no value as an indicator of condition, while plasma proteins, as well as peak corticosterone levels, of starved nestlings indicated ectoparasite load. Triglycerides, of the parameters measured, was the best indicator of the nutritional state of adult Wilson's storm petrels. Our present results may be a basis for future studies of provisioning in seabirds. For example, it would be instructive to study the change in triglyceride levels in adult seabirds following long and short feeding trips. Furthermore, it would be desirable to study haematological parameters in years of contrasting environmental conditions, e.g. years of high and low food availability.

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