

Declining health status of Brown Skua (*Stercorarius antarcticus lonnbergi*) parents and their offspring during chick development

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Abstract During breeding, Brown Skuas (*Stercorarius antarcticus lonnbergi*) perform a great physical effort in the care and maintenance of the nest. Interestingly, the breeding colony on which this work was conducted is in steady decline in recent years. In order to understand the physiological background responsible for the trade off between reproductive effort and health status, in adults and the possible reasons for the colony decline, we evaluated the health status in Brown Skuas parents and growing chicks and blood samples were obtained in three different breeding stages from adults: In (incubation), Er (after egg hatching), and Lr (during chick rearing) and from developing chicks. Serum albumin, α -, β - and γ -globulin fractions, IgY level and corticosterone were determined in adults, while plasma proteins concentration, electrolytes, and γ -globulins were determined in chicks. Differences in albumin, α -, and γ -globulins and IgY levels were observed in adults through the reproductive stages, indicating a

decline in nutritional status and immunocompetence during breeding. In addition, a decline in body condition and immune status was observed in growing chicks, indicating a close relationship between the decrease of the health status and reproductive effort performed by adults and the physiological status of the nestlings during development.

Keywords Reproduction · Immune status · Brown skua (*Stercorarius antarcticus lonnbergi*) · Antarctica

Introduction

Reproduction is one of the greatest physiological constraints in avian life-history (Gustafsson et al. 1994; Hanssen et al. 2005). During this process adult birds have to balance the investment of energy between self-maintenance and feeding and caring for nestlings. To ensure an optimal allocation of resources to competing activities, the resource-limitation hypothesis assumes that under energetic stress there is reduction in the amount of resources available to other systems, such as the immune system, demonstrating a close relationship between reproductive effort, nutritional status, and immunocompetence (Bourgeon and Raclot 2006; Bourgeon et al. 2009).

Increased parental physical demand during incubation and chick rearing may lead to a decline in body condition and immunocompetence, reducing their resistance to infections by parasites and bacteria (Bourgeon and Raclot 2006; Bourgeon et al. 2009). Therefore, regulation of parental reproductive effort in terms of provisioning nestlings is particularly important for longlived seabirds for which foraging at sea and food delivery are energetically expensive behaviors (Chappell et al. 1993; Angelier et al. 2007). Additionally, food provisioning can limit chicks'

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development and survival (Ferrer et al. 2013), but an excessive reproductive effort may decrease parental lifetime, reproductive success, or survival (Croxall and Rothery 1991; Moreno 2003; Ferrer et al. 2013). Altogether, these variables constitute negative factors for the breeding cycle, affecting not only adult and chick survival, but also reducing future fecundity.

The physiological mechanisms responsible for the stress-induced immunosuppression are not fully understood (Bourgeon et al. 2009). Since the endocrine system modulates behavioral and physiological responses to changes in the environment, reduced immunocompetence in breeding animals was suggested to be controlled by changes in hormone secretion (Zuk 1996). Plasma level of corticosterone (glucocorticoid hormone) often is related to changes in body condition and parental effort and in periods of reduced food availability, the raise of plasma corticosterone induces the mobilization of energy stores via protein catabolism (Cherel et al. 1988), and simultaneously enhances foraging behavior and feeding (Wingfield et al. 1998; Lormée et al. 2003). Moreover, previous reports demonstrate the close relationship of corticosterone levels with the decline of immunoglobulin levels and immune responses (Lormée et al. 2003; Bourgeon et al. 2009, 2010).

In seabirds, the simultaneous changes in health status and baseline corticosterone have been studied mainly during incubation when the longest periods of food deprivation occur (Hector and Harvey 1986; Cherel et al. 1988; Hood et al. 1998). Moreover, seabirds in which changes in body condition, immunological status, and corticosterone values have been investigated during the entire breeding cycle, show variation in patterns (Kitaysky et al. 1999; Wingfield et al. 1999). Considering that distinct differences in parental care behavior, particularly during the chick rearing period, may provide a clue to understand the source of variation in the pattern of changes in nutritional and health status (Lormée et al. 2003), and we must enlarge the range of species studied including seabird species that have different patterns of parental care and therefore differ in the energetic constraints that they support during breeding. On the other hand, considering that the way of managing the energy resources by the parents during the reproduction can vary between species, it is important to consider which are the effects on growing chicks and its possible consequences on the reproductive success.

Brown Skuas (*Stercorarius antarcticus lonnbergi*) are longlived top predators that breed in subantarctic islands and the Antarctic (Ritz et al. 2008; Graña Grilli and Montalti 2015). During Antarctic summer Brown Skuas migrate from winter locations in the Atlantic Ocean to Antarctic and subantarctic islands to begin the breeding cycle (Phillips et al. 2007; Krietsch et al. 2017). After arrival, the territory is established almost immediately on

the breeding grounds and 10–30 days after arrival the eggs are laid (Burton 1968). Before the eggs are laid, the male feeds the female to ensure an adequate nutritional condition to conduct the breeding. During the rest of the breeding period too, males undertake a greater share of foraging, whereas females spend a larger part of the time within or close to the territory defending the territory and nestlings against intruders (Burton 1968; Devillers 1978). At Potter Peninsula, the breeding population of this species is decreasing in number and breeding success, and little information is available about the causes of this phenomenon (Graña Grilli 2014). In this work we used hematological parameters to assess the health status in adult and chick Brown Skuas during different breeding and development stages, in order to understand the physiological mechanisms involved in the trade off between reproductive effort, changes in adult health status, and its possible effects on chicks development.

Materials and methods

The study was conducted at Potter peninsula in King George Island/25 de mayo Island, South Shetland Islands, Antarctica (62°15'0"S, 58°40'0"W) from November 2012 to February 2013, when Brown Skuas arrive to begin the breeding cycle. During the summer of 2012, 11 Brown Skua pairs nested but because of a high breeding failure, only four fledged chicks. Therefore we only worked on those four nests where both adults and chicks could be captured ($n = 4$ nests, approximately 40% of the breeding Brown Skua population). To evaluate the immunological status during the breeding cycle in adult and nestling skuas, three reproductive stages were considered: egg incubation (In), early rearing (Er), and late rearing (Lr). The In stage was considered during egg incubation, Er stage immediately after egg hatching, and Lr when the chicks are molting (approximately 30 days old). Chicks were sampled during two stages of development.

Sample collection and hematological tests

Adult Brown Skuas were captured using a net-gun and chicks were extracted from the nest inducing the least possible disturbance so as not to affect the nest in each breeding stage. Blood samples (2 ml from adults and 0.5–1 ml from chicks) were collected by venipuncture of the brachial vein within 3–5 min after bird capture, to avoid changes in biochemical and hematological parameters due to stress associated to handling (Fowler 1999). Blood was incubated for 3 h at 4 °C, and then for serum obtaining, was centrifuged 10 min at 400×g. Serum and red cells for

molecular sexing were frozen at $-20\text{ }^{\circ}\text{C}$ until determinations were performed in the laboratory. To assess nutritional status, albumin concentration in adults and total proteins in chicks were determined using a colorimetric method (Architect, Abbott). Serum protein fractions (α -, β -, and γ -globulins) were analyzed by electrophoresis to evaluate health status. Briefly, agarose gel electrophoresis was performed using a semi-automated equipment (Hydrasis, Sebia electrophoresis, France). After that, gels were stained with 0.2% amido schwarz solution. Finally the electrophoretic profile for each sample was obtained and analyzed using PHORESIS software. Circulating levels of total IgY were determined in serum from adults by direct ELISA using peroxidase-conjugated anti-chicken IgY antibodies (Sigma, St Louis, MO, USA, A-9046). The linear range of the sigmoidal curve for this antibody-antigen response, as well as the optimal serum dilution (1/30,000), were determined as was previously described by Martínez et al. (2003). Serum corticosterone was determined in adults by radioimmunoassays (RIA) as was previously described (Repetto et al. 2010). Finally, electrolytes concentration was determined in serum from chicks using different assays: sodium (100–200 mEq/L), chloride (50–150 mEq/L), and potassium (2–10 mEq/L) with a selective ion analyzer (Konelab 60I Prime, Wiener), and phosphorus (0–60 mg/dl) with a UV method (Konelab 60I prime, Wiener).

Molecular sexing

Sex was determined by polymerase chain reaction (PCR) amplification of a part of two highly conserved genes (CHD) present on the sex chromosomes, as detailed in Weimerskirch et al. (2005).

Statistical analysis

Statistical analysis and plotting were performed using GraphPad Software, Inc. (2007). Normality and homogeneity of variance were tested using Kolmogorov–Smirnov and Levene tests. All compared data were normally distributed and Paired t test (two-tailed) was used to examine differences between males and females during the different breeding stages. Moreover, generalized linear mixed models (GLMM) were performed with the identity of each adult for the different parameters nested in the nest as random effect (X_i) and breeding stage (In, Er and Lr), age and sex as fixed factors (Y_i). The response variables were proteins and phosphorus for chicks, γ -globulins for adults and chicks and albumin, corticosterone, α_1 , α_2 , β and IgY for adults. The analysis were performed using R

software v 3.1.3 (2015) (Core Team 2015) and the package nlme v 3.1-120 (Pinheiro et al. 2015). Results presented in the text for comparisons between sex of adults for each biochemical parameter were expressed as: males or females (breeding stage): mean \pm SE, n and the statistical results as Paired t test, t_{df} , p value, where df = degrees of freedom. GLMM results were summarized in Online Resource 1. A p value less than 0.05 was considered significantly different.

Results and discussion

In this study we analyzed the variation of nutritional and health status parameters in adult and chick Brown Skuas during different breeding and development stages in order to, understand the physiological mechanisms involved in the trade off between reproductive effort, changes in adult health status and its possible effects on chicks development. We have hypothesized that the nutritional and immunocompetence decline in adults, as a consequence breeding effort, could affect offspring development. Moreover, we have consider this hypothesis as a basis to explain the decrease of the breeding population and breeding success reported in this Antarctic region (Graña Grilli 2014). GLMM modeling proved that both parents, as well as offsprings, undergo a significant decline in the nutritional (albumin in adults and plasma proteins and phosphorus in chicks) and immune status (γ -globulins fraction and IgY levels) during the different breeding and development stages. Moreover, parents (regardless of sex) experienced a decrease in body condition in similar magnitudes, indicating that both perform a comparable energy expenditure. Despite the consistency of the results, we observed a trend in the decline of adult's body condition in relation to chick's health status.

During breeding, decline of body condition and immunosuppression occur in order to reallocate resources to other costly functions such as provisioning offspring (Gustafsson et al. 1994; Sheldon and Verhulst 1996; Nordling et al. 1998). Adult Brown Skuas experienced a significant decline in body mass and induce protein catabolism during the breeding stages (Graña Grilli 2015), what is in agreement with the physical effort during egg incubation and early rearing of chicks and the increased foraging activity of males to feed nestlings and females (Burton 1968; Devillers 1978).

In breeding birds, fasting is characterized by a long period of preferential mobilization of fat stores (phase II) followed by a period of increased net protein catabolism (phase III). Of note, serum albumin is a good indicator of nutrition and health in birds (Lumeij 1987). In adult Brown Skuas albumin concentration decreased and no differences

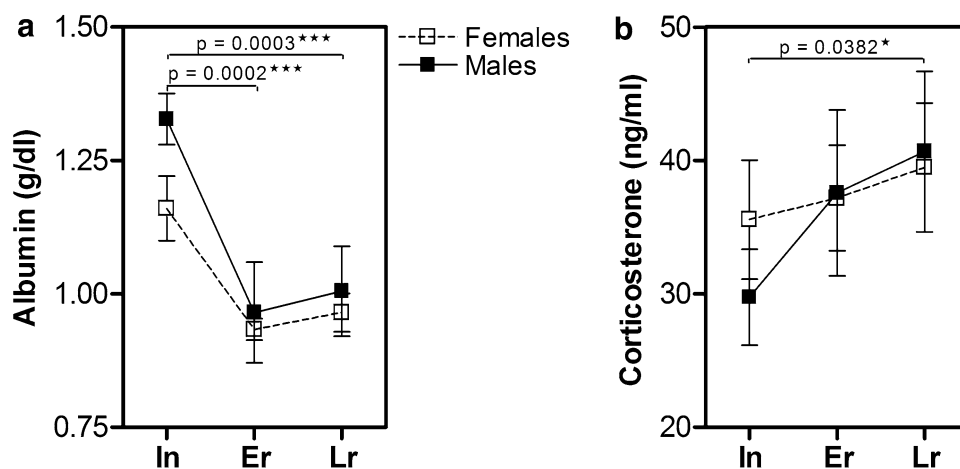
were observed between sexes (Online Resource 1), supporting the decline observed in body condition through the breeding stages (Graña Grilli 2015). Moreover, females and males showed statistically significant differences in albumin concentration [females In: $(1.160 \pm 0.0602 \text{ g/dl}, n = 4)$, Er: $(0.9333 \pm 0.0202 \text{ g/dl}, n = 4)$, Paired t test, $t_3 = 5.152, p = 0.0142$; males In: $(1.328 \pm 0.047 \text{ g/dl}, n = 4)$, Er: $(0.965 \pm 0.0943 \text{ g/dl}, n = 4)$, Paired t test, $t_3 = 4.147, p = 0.0255$ and In: $(1.328 \pm 0.047 \text{ g/dl}, n = 4)$, Lr: $(1.005 \pm 0.084 \text{ g/dl}, n = 4)$, Paired t test, $t_3 = 3.013, p = 0.05$] (Fig. 1a). Phase III is associated to increases of plasmatic corticosterone concentration, which is responsible for the stimulation of protein catabolic pathways for glucose production and energy utilization (Cherel et al. 1988). Together, these results would indicate that adult Skuas experience a decline in serum albumin due to the increasing catabolic activity as a consequence of the energetic stress induced during egg incubation, nest maintenance, and foraging activities, and is positively correlated with the increasing corticosterone concentration during the different stages of breeding (Online Resource 1). Albumin in adult Skuas was lower than reference values previously reported (approximately 1.44 g/dl) (Ibañez et al. 2015). During In stage, albumin in females and males was found below this value, which would indicate that adults were in a suboptimal nutritional condition at the beginning of the breeding cycle, inducing a premature onset of a phase III of fasting (Hollmén et al. 2001).

Immunocompetence in birds is related to the nutritional status and strongly regulated by hormones (glucocorticoids) (Bourgeon et al. 2009, 2010). Energetically costly behaviors reduce the amount of resources available for the immune system (Gustafsson et al. 1994; Bourgeon et al. 2009). As a consequence, immunosuppression may be associated with susceptibility to infections by bacteria or parasites that can affect not only adult's health status, but also the reproductive success and chick's survival

(Deerenberg et al. 1997; Hanssen et al. 2005; Knowles et al. 2009). When exposed to high energetic demands, as during reproduction, the endocrine system increases corticosterone production as an alarm signal, stimulating foraging activity, lipogenesis, and gluconeogenesis under conditions of food scarcity, shifting fat catabolism to protein catabolism (Cherel et al. 1988; Angelier et al. 2007; Bourgeon et al. 2010). Consistently, corticosterone and albumin concentrations in adult Skuas were in agreement indicating that protein catabolism may be stimulated by corticosterone during breeding. An increase in corticosterone concentration between In and Lr stages in adult Skuas was observed (Online Resource 1, Fig. 1b). Additionally, female corticosterone level was higher during the In and Er stages—when egg formation, incubation, and intensive care of the nestling occurs—while in males during Er and Lr, when the effort related to foraging activity and maintenance of the nest increases (Fig. 1b).

Separation of protein fractions (α -, β -, and γ -globulins) by electrophoresis provides information about the physiological status. Relative and total amounts of these protein fractions are affected by infections, inflammatory processes, and nutritional status (Lumeij 1987; Gustafsson et al. 1994). As a consequence of malnutrition, protein deficiency may reduce total protein and albumin concentrations and (or) alter the concentrations of the α - and β -globulin fractions. In addition, its effects on the immunological status may be assessed by determining the γ -globulins amounts (Grasman et al. 2000). Serum protein fractions of Brown Skuas and their reference abundance were previously described. Proteins were scattered in five peaks corresponding to albumin, α_1 , α_2 , β -, and γ -globulin (Ibañez et al. 2015). In this work, adults showed higher values of α_1 - and α_2 globulins than those reported, which may be due to inflammatory processes at the onset of the breeding cycle. A significant increase of the α_1 -globulin fraction between the In–Er stages, while no differences

Fig. 1 Variation in albumin and corticosterone in adult Brown Skuas (*Stercorarius antarcticus lonnbergi*) during the different stages of reproduction (In incubation, Er early rearing and Lr late rearing). Data are represented as mean (\pm SE) for females and males of **a** albumin (g/dl). **b** Corticosterone (ng/ml). Statistical results correspond to the p values calculated by GLMM modeling for adults ($*p < 0.05$ and $***p < 0.001$)



were observed between sexes (Online Resource 1). Female Skuas showed higher values of α_1 -globulin fraction (In: 1.06 ± 0.0348 g/dl, $n = 4$, Er: 1.353 ± 0.1223 g/dl, $n = 4$, Paired t test, $t_3 = 3.266$, $p = 0.0469$ and In: 1.06 ± 0.0348 g/dl, $n = 4$, Lr: 1.235 ± 0.02363 g/dl, $n = 4$, Paired t test, $t_3 = 4.193$, $p = 0.0247$) (Fig. 2a) and no increase was observed in α_2 -globulins (Fig. 2b). β -globulins decreased in adults during the different breeding stages (Fig. 2c, Online Resource 1).

On the other hand, a decrease in humoral immune responses (as a drop in γ -globulins) was observed in adult Skuas during breeding. GLMM modeling (with age and breeding stage as fixed effects) showed differences in this parameter only in adults through the breeding stages, while considering the effect of age, no significant correlation was observed between adults and chicks (Fig. 2d, Online Resource 1). Moreover, differences were observed in both sexes (females In: 0.2825 ± 0.02562 g/dl, $n = 4$, Er: 0.22 ± 0.0219 g/dl, $n = 4$, Paired t test, $t_3 = 13.06$, $p = 0.001$; males In: 0.29 ± 0.0336 g/dl, Er:

0.1575 ± 0.0103 g/dl, $n = 4$, Paired t test, $t_3 = 3.666$, $p = 0.0351$ and In: 0.29 ± 0.0336 g/dl, Lr: 0.1575 ± 0.0256 g/dl, Paired t test, $t_3 = 3.714$, $p = 0.0340$) through the breeding stages. These results indicate that adult Skuas undergo a dysproteinemia during breeding, by means of a decline in albumin, β - and γ -globulin fractions and an increase in α -globulins. Supporting this observation, albumin/globulin ratio (A/G ratio) values decreased in adults during the breeding cycle (females In: 0.5533 ± 0.02901 , Er: 0.4133 ± 0.0088 , $n = 4$, Paired t test, $t_3 = 4.583$, $p = 0.0445$; males In: 0.5750 ± 0.0290 , Er: 0.4667 ± 0.04910 , $n = 4$, Paired t test, $t_3 = 10$, $p = 0.0099$ and In: 0.5750 ± 0.0290 , Lr: 0.5125 ± 0.0233 , $n = 4$, Paired t test, $t_3 = 4.753$, $p = 0.0177$) (Fig. 2e, Online Resource 1). Furthermore, a significant decline in IgY level was observed in adult Skuas (Fig. 2f, Online Resource 1). Altogether, the differences observed in adult's immunological status indicate that the extent of immunosuppression was higher in female Brown Skuas during the phases of incubation and early care of chicks, while in

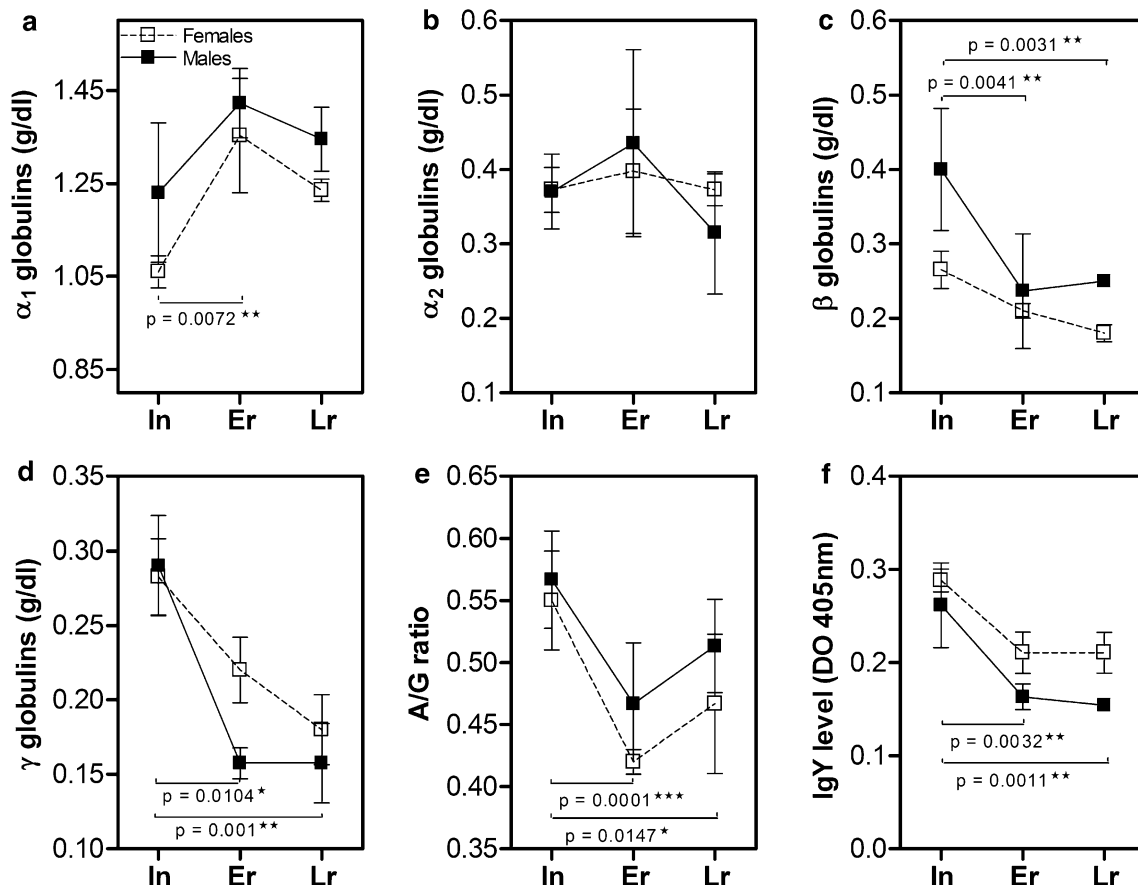


Fig. 2 Immunological status in adult Brown Skuas during breeding. Data are represented as mean (\pm SE) of each serum protein fraction for females and males. **a** α_1 -globulins (g/dl). **b** α_2 -globulins (g/dl). **c** β -globulins (g/dl). **d** γ -globulins (g/dl). **e** A/G ratio. **f** IgY level (DO at

405 nm). Statistical results correspond to the p values calculated by GLMM modeling for adults ($*p < 0.05$, $**p < 0.01$ and $***p < 0.001$)

males during the entire course of the reproduction, it can be related to the elevated foraging behavior and physical effort performed to maintain the nest.

Under energetic stress, sometimes, parents cannot fully compensate for the increased food demand of the nestlings (Ferrer et al. 2013). Food provisioning involves two processes: resource acquisition and resource allocation between self-maintenance and offspring's demands (Viñuela et al. 1996; Weimerskirch 1999). Balance between both processes eventually determines the reproductive success of individuals. We observed a decline in body condition and health status of chicks in development. Plasma proteins (Er: 2.890 ± 0.242 g/dl, Lr: 2.465 ± 0.110 g/dl, $n = 4$), γ -globulins (Er: 0.1450 ± 0.085 g/dl, Lr: 0.0875 ± 0.017 g/dl, $n = 4$) and phosphorus (Er: 6.810 ± 0.370 mg/dl, Lr: 4.710 ± 0.098 mg/dl, $n = 4$, Paired t test, $t_3 = 6.458$, $p = 0.0075$) (Online Resource 1, Fig. 3) levels dropped compared with reference values previously reported (Ibañez et al. 2015). Despite of the decline of the nutritional and health status in adults, because the reproductive effort,

the suboptimal level in hematological parameters of chicks demonstrates that development was deteriorated, which may have direct consequences on the reproductive success of this specie. GLMM results on immune status showed a slight relationship in decline of adult's and chick's immunocompetence, so considering this, we are not able to assure that decline in parent's body condition may directly affects chicks growth.

In this physiological context, maintaining low energy reserves in breeding Brown Skuas would affect the adaptive capacity to changes in the environment as well as reduced survival and/or fecundity in subsequent breeding attempts (Røskaft 1985; Gustafsson and Sutherland 1988; Hahn et al. 2007; Ferrer et al. 2013). We do not know if the deterioration of parent's health status because of the greater foraging activity and allocation of resources in their chicks, would have consequences in future breeding attempts. Neither do we know what effect of this allocation activity would have in the survival and future fitness of their young (Noordwijk and de Jong 1986; Råberg et al. 1998). The physiological deterioration on adults could be a

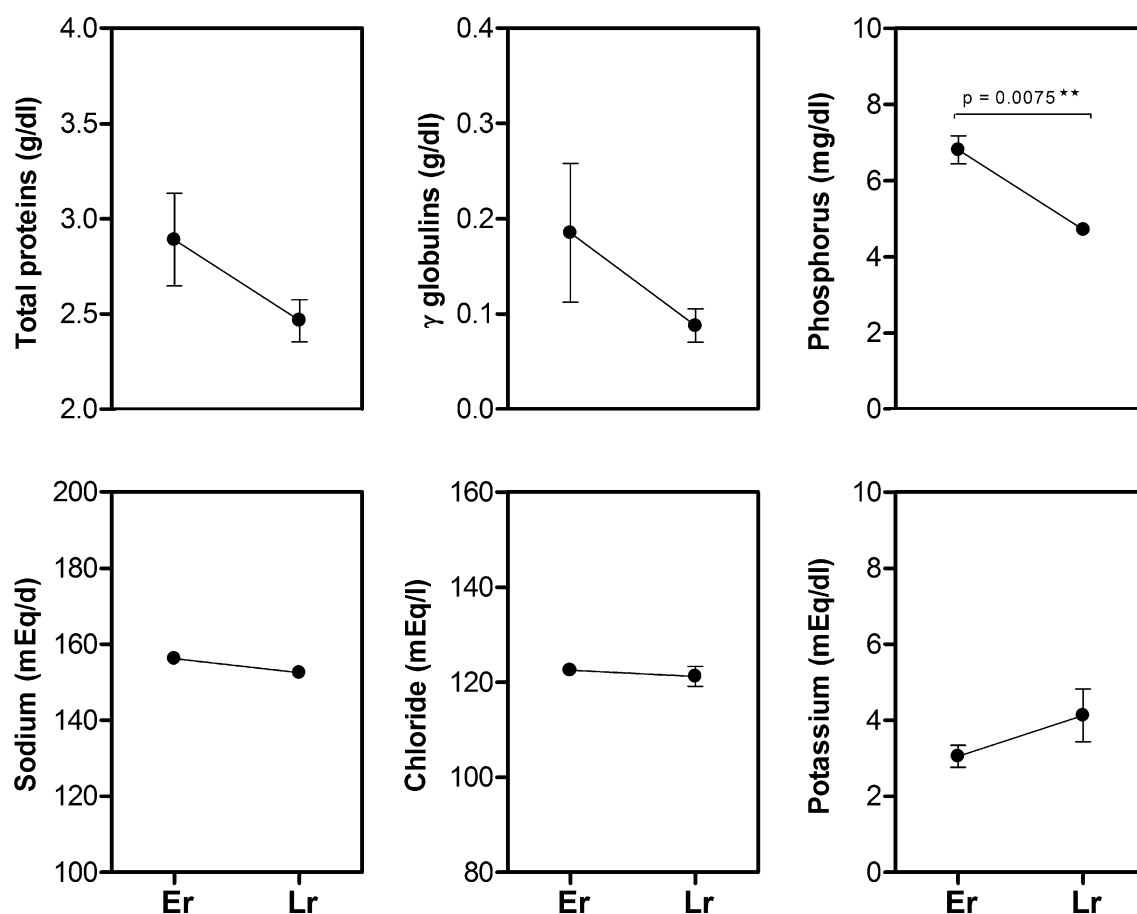


Fig. 3 Nutritional and health status in growing Brown Skua chicks. Data are represented as mean (\pm SE) of total proteins (g/dl), γ -globulins (g/dl), and electrolytes [phosphorus (mg/dl), sodium (mEq/

l), chloride (mEq/l), and potassium (mEq/l)]. Statistical results correspond to the p values calculated by GLMM modeling for chicks (** $p < 0.01$)

consequence of the onset of reproduction under suboptimal nutritional or health conditions, which also may be related to the availability and quality of food at wintering and breeding locations. Additional long-term work on the same individuals would be necessary to understand how this trade off is resolved and which could be the cause of the decline in numbers, combined with, annual census of breeding pairs in this location and studies on the quality and food resources availability, as well as reproductive success studies. Altogether, this information contributes to our knowledge on physiology and the overall health status of this specie, which will substantially aid in future conservation efforts.

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