Polar Biol (2018) 41:193–200
DOI 10.1007/s00300-017-2181-5

SHORT NOTE

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

Andrés Esteban Ibañez[1] · Maricel Graña Grilli[2] · Amalia Figueroa[3] · Marcela Pari[3] · Diego Montalti[1,4]

Received: 31 January 2017 / Revised: 8 July 2017 / Accepted: 12 July 2017 / Published online: 5 August 2017

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

Electronic supplementary material The online version of this article (doi:10.1007/s00300-017-2181-5) contains supplementary material, which is available to authorized users.

✉ Andrés Esteban Ibañez
aeibanez@fcnym.unlp.edu.ar

1 Sección Ornitología, Div. Zool. Vert., Museo de la Plata (FCNyM-UNLP, CONICET), Paseo del Bosque s/n la Plata (B1900FWA), Buenos Aires, Argentina

2 Grupo de Investigaciones en Biología de la Conservación, Laboratorio Ecotono, INIBIOMA (Universidad Nacional del Comahue-CONICET), San Carlos de Bariloche, Argentina

3 Laboratorio de Análisis Clínicos y Bioquímicos del Hospital Interzonal General de Agudos (HIGA) Luisa C. Gandulfo, Buenos Aires, Argentina

4 Instituto Antártico Argentino (IAA), Capital Federal, Argentina

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' 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 $400\times g$. Serum and red cells for molecular sexing were frozen at −20 °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 schwartz 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 ± 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 ± 0.0602 g/dl, $n = 4$), Er: (0.9333 ± 0.0202 g/dl, $n = 4$), Paired t test, $t3 = 5.152$, $p = 0.0142$; males In: (1.328 ± 0.047 g/dl, $n = 4$), Er: (0.965 ± 0.0943 g/dl, $n = 4$), Paired t test, $t3 = 4.147$, $p = 0.0255$ and In: (1.328 ± 0.047 g/dl, $n = 4$), Lr: (1.005 ± 0.084 g/dl, $n = 4$), Paired t test, $t3 = 3.013$, $p = 0.05$] (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 gluconeogensis 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

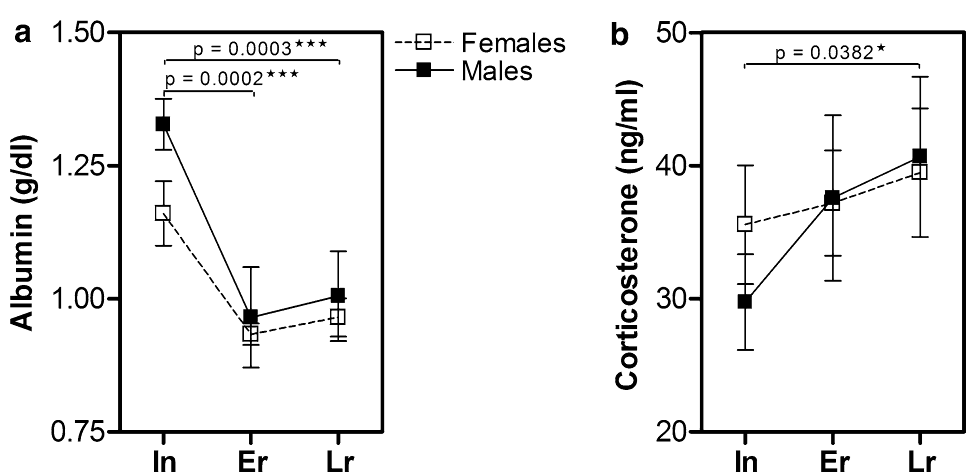

Fig. 1 Variation in albumin and corticosterone in adult Brown Skuas (*Stercorarius antarcticus lonnbergi*) during the different stages of reproduction (*In* incubation, *Er* early rearing and *Lr* late rearing). Data are represented as mean (±SE) for females and males of **a** albumin (g/dl). **b** Corticosterone (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, $t3 = 3.266$, $p = 0.0469$ and In: 1.06 ± 0.0348 g/dl, $n = 4$, Lr: 1.235 ± 0.02363 g/dl, $n = 4$, Paired t test, $t3 = 4.193$, $p = 0.0247$) (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, $t3 = 13.06$, $p = 0.001$; males In: 0.29 ± 0.0336 g/dl, Er: 0.1575 ± 0.0103 g/dl, $n = 4$, Paired t test, $t3 = 3.666$, $p = 0.0351$ and In: 0.29 ± 0.0336 g/dl, Lr: 0.1575 ± 0.0256 g/dl, Paired t test, $t3 = 3.714$, $p = 0.0340$) 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, $t3 = 4.583$, $p = 0.0445$; males In: 0.5750 ± 0.0290, Er: 0.4667 ± 0.04910, $n = 4$, Paired t test, $t3 = 10$, $p = 0.0099$ and In: 0.5750 ± 0.0290, Lr: 0.5125 ± 0.0233, $n = 4$, Paired t test, $t3 = 4.753$, $p = 0.0177$) (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

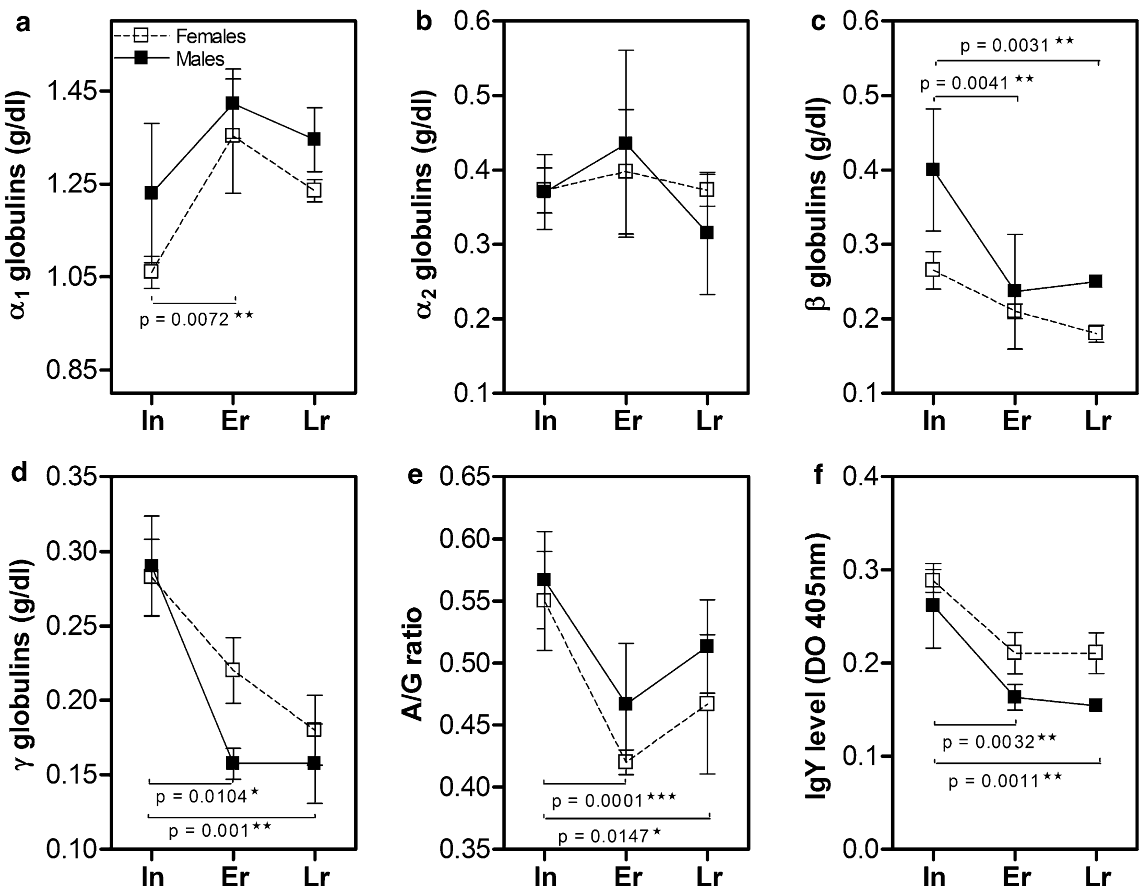

Fig. 2 Immunological status in adult Brown Skuas during breeding. Data are represented as mean (±SE) of each serum protein fraction for females and males. **a** α_1-globulins (g/dl). **b** α_2-globulins (g/dl). **c** β-globulins (g/dl). **d** γ-globulins (g/dl). **e** A/G ratio. **f** IgY level (DO at 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, $t3 = 6.458$, $p = 0.0075$) (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

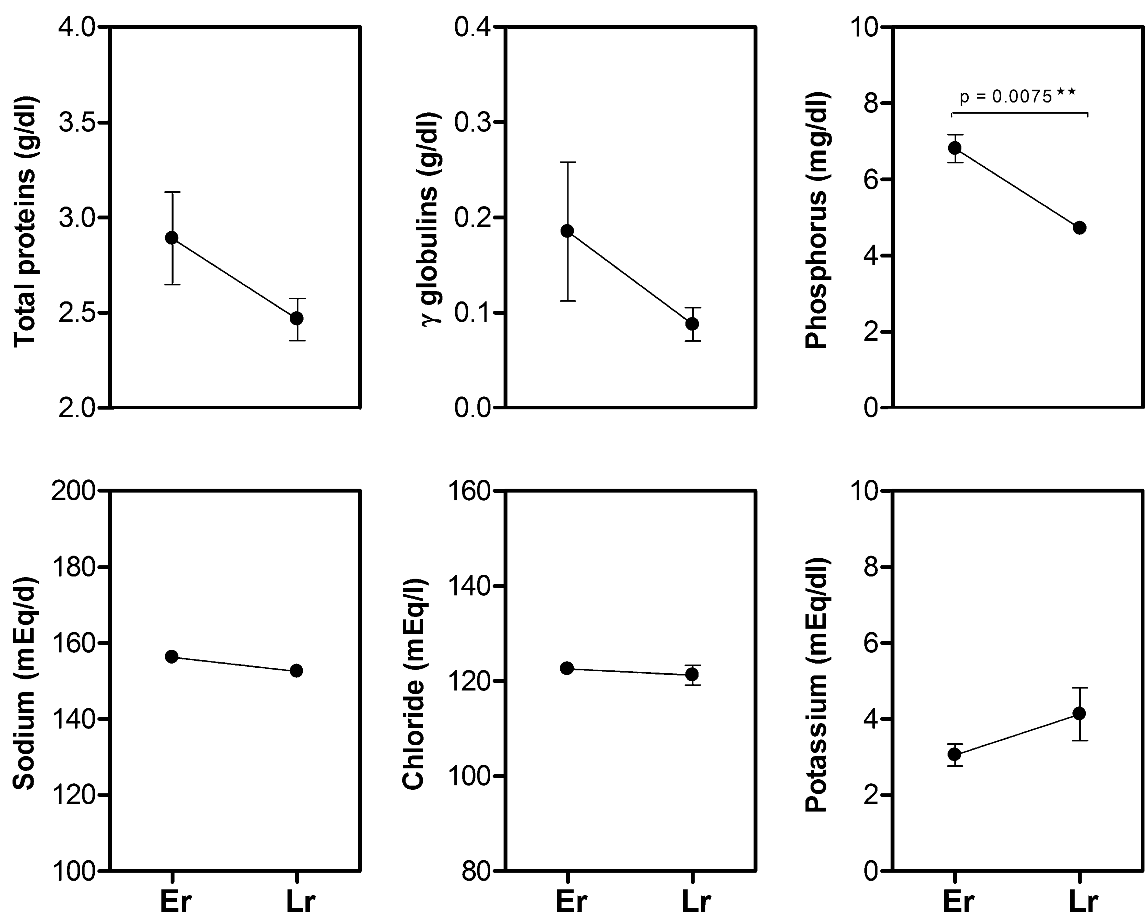

Fig. 3 Nutritional and health status in growing Brown Skua chicks. Data are represented as mean (±SE) of total proteins (g/dl), γ-globulins (g/dl), and electrolytes [phosphorus (mg/dl), sodium (mEq/l), chloride (mEq/l), and pottasium (mEq/l)]. Statistical results correspond to the p values calculated 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.

Acknowledgments This work was made possible thanks to Instituto Antártico Argentino (IAA), which provided logistical support and permission to carry out the fieldwork at Potter Peninsula. This work was supported by Proyecto de Investigación Plurianual (PIP- CONICET n:0158) and Agencia Nacional de Promoción Científica y Tecnológica and Instituto Antártico Argentino (PICTA-2010-0080) (To Diego Montalti) and partially supported by (PICT-2014-3323) (to AEI). Special thanks to Juan Manuel Girini and Facundo Xavier Palacio for their help with statistical analysis, as well as to the Editor and reviewers for their interesting and helpful critics of the manuscript.

References

Angelier F, Shaffer SA, Weimerskirch H, Trouvé C, Chastel O (2007) Corticosterone and foraging behavior in a pelagic seabird. Physiol Biochem Zool 80:283–292

Bourgeon S, Raclot T (2006) Corticosterone selectively decreases humoral immunity in female eiders during incubation. J Exp Biol 209:4957–4965

Bourgeon S, Le Maho Y, Raclot T (2009) Proximate and ultimate mechanisms underlying immunosuppression during the incubation fast in female eiders: roles of triiodothyronine and corticosterone. Gen Comp Endocrinol 163:77–82

Bourgeon S, Kauffmann M, Geiger S, Raclot T, Robin JP (2010) Relationships between metabolic status, corticosterone secretion and maintenance of innate and adaptive humoral immunities in fasted re-fed mallards. J Exp Biol 213:3810–3818

Burton RW (1968) Breeding biology of the Brown Skua *Catharacta skua lonnbergi* (Mathews), at Signy Island, South Orkney Islands. Br Antarct Surv Bull 15:9–28

Chappell MA, Shoemaker VH, Janes DN, Maloney SK, Bucher TL (1993) Energetics of foraging in breeding adélie penguins. Ecology 74:2450–2461

Cherel Y, Robin JP, Walch O, Karmann H, Netchitailo P, Le Maho Y (1988) Fasting in king penguins I. Hormonal and metabolic changes during breeding. Am J Physiol 254:170–177

Core Team R (2015) R: A language and environment for statistical computing. R foundation for statistical computing, Viena, Autria. http://www.R-project.org/

Croxall JP, Rothery P (1991) Population regulation of seabirds: implications of their demography for conservation. In: Perrins CJ, Lebreton JD, Hirons GJM (eds) Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, pp 272–296

Deerenberg C, Arpanius V, Daan S, Bos N (1997) Reproductive effort decreases antibody responsiveness. Proc R Soc Lond B 264:1021–1029

Devillers P (1978) Distribution and relationships of South American Skuas. Éditions du Gerfaut, Paris

Ferrer M, Belliure J, Viñuela J, Martin B (2013) Parental physiological condition and reproductive success in chinstrap penguins (*Pygoscelis antarctica*). Polar Biol 36:529–535

Fowler GS (1999) Behavioral and hormonal responses of magellanic penguins to tourism and nest site visitation. Biol Conserv 90:143–149

Graña Grilli M (2014) Decline in numbers of Antarctic Skuas breeding at Potter Peninsula, King George Island, Antarctica. Mar Ornithol 42:161–162

Graña Grilli M (2015) Uso del espacio, dieta y estado corporal del skua pardo (*Stercorarius antarcticus lonnbergi*) durante su período reproductivo en Antártida. Doctoral Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata

Graña Grilli M, Montalti D (2015) Variation in diet composition during the breeding cycle of an Antarctic seabird in relation to its breeding chronology and that of its main food resource. Polar Biol 38:643–649

Grasman KA, Armstrong M, Hammersley DL, Scanlon PF, Fox GA (2000) Geographic variation in blood plasma protein concentrations of young herring gulls (*Larus argentatus*) and caspian terns (*Sterna caspia*) from the Great Lakes and Lake Winnipeg. Comp Biochem Physiol C 125:365–375

Gustafsson L, Sutherland WJ (1988) The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335:813–815

Gustafsson L, Nordling D, Andersson MS, Sheldon BC, Quarnstrøm A (1994) Infectious disease, reproductive effort and the cost of reproduction in birds. Philos Trans R Soc Lond B 346:323–331

Hahn S, Reinhardt K, Ritz MS, Janicke T, Montalti D, Peter H-U (2007) Oceanographic and climatic factors differentially affect reproduction performance of Antarctic skuas. Mar Ecol Prog Ser 334:287–297

Hanssen SA, Hasselquist D, Folstad I, Erikstad KE (2005) Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proc R Soc Lond B 272:1039–1046

Hector JA, Harvey S (1986) Corticosterone secretion through long incubation shifts in Diomedea albatrosses. Gen Comp Endocrinol 62:349–352

Hollmén T, Franson JC, Hario M, Sankari S, Kilpi M, Lindström K (2001) Use of serum biochemistry to evaluate nutritional status and health of incubating common eiders (*Somateria mollissima*) in Finland. Physiol Biochem Zool 74:333–342

Hood LC, Boersma PD, Wingfield JC (1998) The adrenocortical response to stress in incubating magellanic penguins (*Spheniscus magellanicus*). Auk 115:76–84

Ibañez AE, Najle R, Larsen K, Montalti D (2015) Hematology, biochemistry and serum protein analyses of Antarctic and non-Antarctic skuas. Waterbirds 38:153–161

Kitaysky AS, Wingfield JC, Piatt JF (1999) Dynamics of food availability, body condition and physiological response in breeding black-legged kittiwakes. Funct Ecol 13:577–585

Knowles SCL, Nakagawa S, Sheldon BC (2009) Elevated reproductive effort increases blood parasitaemia and decreases immune function in birds: a meta-regression approach. Funct Ecol 23:405–415

Krietsch J, Hahn S, Kopp M, Phillips RA, Peter HU, Lisovski S (2017) Consistent variation in individual migration strategies of Brown Skuas. Mar Ecol Prog Ser. doi:10.3354/meps11932

Lormée H, Jouventin P, Trouve C, Chastel O (2003) Sex-specific patterns in baseline corticosterone and body condition changes in breeding red-footed boobies *Sula sula*. Ibis 145:212–219

Lumeij JT (1987) The diagnostic value of plasma proteins and non-protein nitrogen substances in birds. Vet Q 9:262–268
Martínez J, Tomás G, Merino S, Arriero E, Moreno J (2003) Detection of serum immunoglobulins in wild birds by direct ELISA: a methodological study to validate the technique in different species using antichicken antibodies. Funct Ecol 17:700–706
Moreno J (2003) Lifetime reproductive success in seabirds: interindividual differences and implications for conservation. Sci Mar 67:7–12
Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142
Nordling D, Andersson M, Zohari S, Gustafsson L (1998) Reproductive effort reduces specific immune response and parasite resistance. Proc R Soc Lond B 265:1291–1298
Phillips R, Catry P, Silk J, Bearhop S, McGill R, Afanasyev V, Strange I (2007) Movements, winter distribution and activity patterns of falkland and Brown Skuas: insights from loggers and isotopes. Mar Ecol Prog Ser 345:281–291
Pinheiro J, Bates D, Debroy S, Sarkar D, R Core Team (2015) nlme: linear and nonlinear mixed effects models. R package version 3.1-120. http://CRAN.R-project.org/package=nlme>
Råberg L, Grahn M, Hasselquist D, Svensson E (1998) On the adaptive significance of stress-induced immunosuppression. Proc R Soc Lond B 265:1637–1641
Repetto EM, Sanchez R, Cipelli J, Astort F, Martinez Calejman C, Piroli GG, Arias P, Cymeryng CB (2010) Dysregulation of corticosterone secretion in streptozotocin-diabetic rats: modulatory role of the adrenocortical nitrergic system. Endocrinology 151:203–210
Ritz M, Millar C, Miller G, Phillips R, Ryan P, Sternkopf V, Liebers-Helbig D, Hans-Ulrich P (2008) Phylogeography of the southern skua complex-rapid colonization of the southern hemisphere during a glacial period and reticulate evolution. Mol Phylogenet Evol 49:292–303
Røskaft E (1985) The effect of enlarged brood size on future reproductive potential on the rook. J Anim Ecol 54:255–260
Sheldon BC, Verhulst S (1996) Ecological immunology: costly parasite defenses and trade-offs in evolutionary ecology. Trends Ecol Evol 11:317–321
Viñuela J, Moreno J, Carrascal LM, Sanz JJ, Ferrer M, Amat JA, Belliure J, Cuervo JJ (1996) The effect of hatching date on parental care, chick growth and chick mortality in the chinstrap penguin *Pygoscelis antarctica*. J Zool Lond 240:51–58
Weimerskirch H (1999) The role of body condition on breeding and foraging decisions in albatrosses and petrels. In: Adams NJ, Slotow RH (eds) Proceedings of 22 international ornithological congress. Durban, Johannesburg, pp 1178–1189
Weimerskirch H, Lallemand J, Martin J (2005) Population sex ratio variation in a monogamous long-lived bird, the wandering albatross. J Animal Ecol 74:285–291
Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD (1998) Ecological bases of hormone-behavior interactions: the ‘‘emergency life history stage’’. Amer Zool 38:191–206
Wingfield JC, Ramos-Fernandez G, Nuñez De La Mora A, Drummond H (1999) The effects of an ‘El Niño’ southern oscillation event on reproduction in male and female Bluefooted Boobies, *Sula nebouxii*. Gen Comp Endocrinol 114:163–172
Zuk M (1996) Disease, endocrine-immune interactions and sexual selection. Ecology 77:1037–1042