



Poor body conditions during the breeding period in a seabird population with low breeding success

Maricel Graña Grilli¹ · Marcela Pari² · Andrés Ibañez³

Received: 2 February 2018 / Accepted: 10 August 2018 / Published online: 17 August 2018
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

Breeding has a high energetic cost and, in central place foragers, also restricts the ability of parents for self-foraging, with affecting on their body and immunological conditions. In migratory species, breeding overlaps the period of recovery of body conditions before the following outbound migration. Those factors may reduce the breeding success and even lead parents to abandon their offspring if parental body condition cannot guarantee the success of the next migration. We studied the body and immunological conditions of a low breeding success population of Brown Skuas (*Stercorarius antarcticus lonnbergi*) throughout their breeding season. We evaluated changes in their body mass, blood parameters and heterophil:lymphocyte ratios (*H:L*), at three stages of their breeding period: Incubation, Early rearing and Late rearing. The body mass of female Brown skuas decreased during the initial stages of the breeding period and recovered towards the end. The changes in metabolites suggest a use of protein body reserves but not of lipid reserves. The *H:L* ratio did not indicate changes in the immune condition of the birds. Our results suggest that this low breeding success population begins its breeding period with a poor body condition that it continues to decline throughout the season. Those poor body conditions added to the need for recovery for the next migration may be the cause of the abandonment of almost totally feathered chicks. Our evidence highlights the importance of food availability, in either the breeding or wintering sites, or both, on the health of the populations of migratory top predators.

Introduction

The body condition of birds is the result of a dynamic interaction between the physiological state, health, energetic requirements and the amount and quality of the food (Murphy 1996). Breeding is a stage in the life cycle with a high degree of stress and energetic cost (Williams 1966) caused,

among others, by the physiological cost of egg production and the activities related to caring and feeding the offspring (Kalmbach et al. 2004; Harding et al. 2011; Mitchell et al. 2012). Because of the physiological cost of egg production in females and, due to differences in the rearing activities and investment between sexes (Weimerskirch and Lys 2000; Weimerskirch et al. 2009; Hennicke et al. 2015), the cost of reproduction may differ in males and females. In addition, the movements of birds feedback with the body condition, through both the influence over each other and on the food that parents are able to obtain (Tveraa et al. 1998; Nathan et al. 2008). Therefore, in central place foragers, breeding also influences the body condition through the restriction that imposes to the movements of parents (Bertoldi Carneiro et al. 2015), as well as through the reduction in their time for self-feeding (Weimerskirch 1990).

Energy invested by parents in the breeding activities increases as the offspring grow and increase their energetic requirements (Drent and Daan 1980; Weimerskirch et al. 2000). Such investment in offspring has negative effects on the body condition of parents, in a magnitude that increases throughout the breeding period and with the

Responsible Editor: Y. Cherel.

Reviewed by J-P. Robin and an undisclosed expert.

✉ Maricel Graña Grilli
ggmaricel@comahue-conicet.gov.ar

¹ Grupo de Investigaciones en Biología de la Conservación, Laboratorio Ecotono, INIBIOMA (Universidad Nacional del Comahue, CONICET), Pasaje Gutierrez 1125 (R8400FRF), San Carlos de Bariloche, Argentina

² Laboratorio de Análisis Clínicos y Bioquímicos del Hospital Interzonal General de Agudos (HIGA) Luisa C. Gandulfo, Buenos Aires, Argentina

³ Sección Ornitología, Div. Zool. Vert., Museo de la Plata (FCNyM-UNLP), La Plata, Argentina

offspring size (Drent and Daan 1980; Weimerskirch 1990; Kalmbach et al. 2004; Mitchell et al. 2012), and may also compromise the future survivorship of parents (Harding et al. 2011). In some species, particularly in long-lived ones, the parents may abandon their offspring when their body conditions drop below a limit that compromises their survivorship and future breeding (Chaurand and Weimerskirch 1994; Gauthier-Clerc et al. 2001; Groscolas et al. 2008).

In migratory birds, the breeding period is preceded and followed by a migration, which often means that in addition to the energetic expenditure related to breeding, the birds must recover their body condition after the previous migration and prepare for the next one. Such migratory movements are energetically demanding, involve the use of body reserves, and require a recovery period both after the migration and during stopovers (Guglielmo et al. 2005; Lyons et al. 2008; Seewagen et al. 2011). The breeding success is influenced by the body conditions of parents both before and during the breeding period. Therefore, migratory species may be under more demanding conditions for reproduction than resident ones (Drent and Daan 1980; Boersma and Ryder 1983; Gustafsson et al. 1994; Selman and Houston 1996; Machado-Filho et al. 2010). Energy destined to supply those demands of the reproductive cycle can be subsidised by food resources obtained during the current breeding period—*income breeders*—, or by body reserves stored before the breeding period—*capital breeders* (Stephens et al. 2009) at different distances from the breeding grounds—*distant capital* or *local capital breeders* (Klaassen et al. 2006).

The stress generated by those different moments in the life cycle as well as by environmental factors stimulates the release of glucocorticoid hormones to the blood (Harvey et al. 1984; Ouyang et al. 2011), which produces a negative effect on the body and immunological conditions (Marra and Holberton 1998; Cirule et al. 2012; Kuluszewicz et al. 2017). Body condition can be evaluated through different aspects such as morphological features as fat and muscle reserves (Carrascal et al. 1998; Rae et al. 2009), hematological and biochemical parameters (Masello and Quillfeldt 2004; Smith et al. 2007; Minias 2014). Fat and muscle stores are energy reserves that can be used in case of an insufficient energetic income from the diet. Fat reserves have fast formation and utilisation according to immediate needs, while protein reserves are more difficult to mobilise and are, therefore, considered as long-term indicators of body conditions (Carrascal et al. 1998). Energy readily available from either the diet, mobilisation of body reserves, or both is found in the blood as glucose. The immunological condition is also an indicator of general body condition (Norris and Evans 2000; Machado-Filho et al. 2010; Kuluszewicz et al. 2017) as the immune activation requires energetic reserves (Moreno-Rueda 2011) and is negatively influenced by food shortage

as well as by breeding activities (Norris and Evans 2000; Kuluszewicz et al. 2017).

Potter Peninsula, at King George Island, Antarctica, is a breeding ground for Brown Skuas (*Stercorarius antarcticus lonnbergi*). The population breeding there probably winters in a wide range in the west-Atlantic, reaching as north as the South Brazil Shelf (Krietsch et al. 2017). Throughout the breeding period, parents must recover their body conditions after the spring migration in order to successfully and to be prepared for the following outbound migration. At the moment of this study, the breeding success of Brown Skuas at this site was very low (Graña Grilli 2014) and some chicks were seen abandoned to starvation even after complete feathering (pers. obs.). Low breeding success in a population can be related with suboptimal conditions of breeders, and the aim of this work was to study the body and immunological conditions of Brown Skuas throughout their breeding season at this locality.

Materials and methods

Sampling

The study was carried out in Potter Peninsula, King George Island, Antarctica (62°15'S, 58°40'W) during the austral summers 2012/13 (11 pairs) and 2013–14 (10 pairs). The breeding period was divided into three stages: (1) incubation (In), (2) early rearing (Er) and (3) late rearing (Lr) (Ibañez et al. 2018). For In, the sampling was done 10–13 days after the egg was found. For Er, the trapping was done about 10–13 days after the chick was found (chicks were found no later than 3 days after hatching). The Lr stage started when the chicks were completely feathered but still not flying (about 40 days old). During the season 2012/13, 6 pairs lost their eggs at the In stage while 5 got to hatch chick and only 3 of them got to fledge chicks. During the season 2013–14, 6 of the studied pairs lost their eggs at In, 4 got to hatch chicks and 2 of them fledged chicks (see Graña Grilli 2014).

At each one of the defined stages, both members of each breeding pair were captured for extraction of a 2 ml blood sample from the brachial vein and record of their body mass (± 20 g). One drop of blood was used to make a smear and the remaining was kept in tubes with sodic heparin to avoid coagulation. At laboratory, plasma was obtained by centrifugation at 3500 rpm and kept frozen (-20 °C) until analysis in Laboratorio de Análisis Clínicos y Bioquímicos (HIGA Gandulfo). Body mass was also recorded at the beginning (S) of incubation, as soon as the eggs were found. The birds were sexed by molecular techniques (Griffiths et al. 1998).

To assess an effect of the location of the nest relative to the main source of food, the proximity of the nest of each studied skua pair to the penguin colonies also was measured

and compared among birds that lost their nest during the In stage and those that succeed to hatch chicks. Because the sampled birds also were tagged with GPS loggers and the home range was calculated for each bird, the proximity was measured using ArcGIS 10.1, as the lineal distance from the nest to the nearest border of the closest penguin sub-colony included in the kernel density estimation 95% of each bird during the In stage (unpub. data).

Hematological parameters

The concentration of metabolites associated with metabolic pathways of protein and lipids as well as that of glucose as a source of readily available energy was determined in plasma. To this end, enzymatic assays were carried out on simple samples using a high precision automatic analyser Architect i2000 (Abbott Diagnostics, Illinois, USA). Total proteins, urea and uric acid were the parameters related to the metabolic path of proteins analysed; and triglycerides and non-esterified fatty acids (NEFA, Randox, USA) were those related to the metabolic path of lipids.

Urea and uric acid are products of protein catabolism and can result from either the use of internal reserves or the metabolism of food proteins (Cherel and Le Maho 1985; Alonso-Alvarez et al. 2002). On the other hand, total proteins are positively related to nutritional conditions (Gustafsson et al. 1994). Therefore, the coupled analysis of these three parameters allows determining whether the bird is using its own protein body reserves or getting proteins from the diet. On the other hand, fat ingested in food as triglycerides (Guglielmo et al. 2005) is split up in the gut producing NEFA and monoacylglycerol that cross the gut wall and in the blood stream re-synthesise triglycerides. Contrariwise, triglycerides contained in the cells of fat stores are hydrolysed producing NEFA that are released to the blood stream and transported to the muscle cells (Price 2010). Therefore, the concentrations of triglycerides and NEFA in plasma are indicators of fat stores formation and utilisation (Guglielmo et al. 2005; Price 2010).

Leucocyte counts

Blood smears were fixed by immersion in methanol for 3 min and air dried and then stained with Wright colourant. Stained smears were examined in microscope (1000 \times) under immersion oil and a sample of 100 leucocytes was counted and classified as lymphocytes, heterophils, eosinophils, basophils and monocytes (Campbell 1994). From those numbers, the ratio heterophil:lymphocyte ($H:L$) was calculated (Davies et al. 2008; Lebigre et al. 2012).

The $H:L$ ratio obtained from the leucocitary profile is an indicator of the health status of birds (Cirule et al. 2012). Glucocorticoids induce the release of heterophils into the

bloodstream and preclude them of leaving it and, at the same time, induce the adhesion of lymphocytes to the blood vessels wall and then their pass to other tissues (Davies et al. 2008; Cirule et al. 2012). For this reason, the $H:L$ ratio increases under stressing conditions, such as during breeding (Norris and Evans 2000; Antonio-Garcia et al. 2010) and low food availability (Machado-Filho et al. 2010).

Data analysis

We used GLMM to analyse the variation of each variable according to the stage of the breeding period and the sex of the birds. The identity of the bird and the season were considered random effects. A different effect of the breeding stage according to the sex of the bird was also studied. We used the lme function in the nlme package of the software R (R Core Team. 2014). The influence of the distance between the nest and the penguin colony was analysed through a GLMM for binomial distribution using the identity of the pair as the random effect in the glmer function in the lme4 package (R Core Team 2014). Results are presented as mean \pm SD and were considered significant at alpha values ≤ 0.05 .

Results

Laying dates were similar in both seasons, taking place between 23 November and 22 December in the season 2012/13 and between 20 November and 28 December in the season 2013/14. The date of laying was not related to the body mass of males ($t = 1.70$, $P = 0.13$) or females ($t = 0.40$, $P = 0.70$) (Fig. 1). The mean distance between the nest and the nearest border of a penguin colony included in the home range of the bird was 7.42 m (± 4.82 m) and did not change

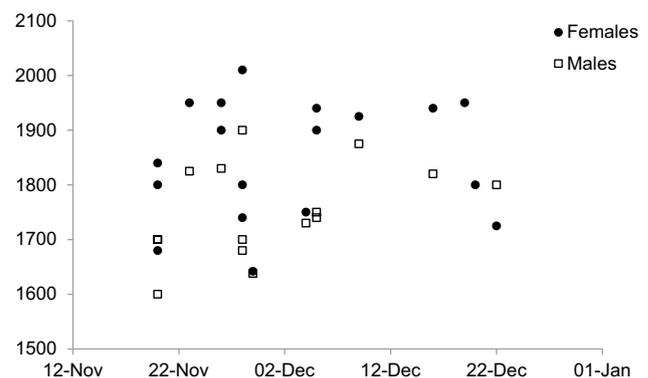


Fig. 1 Body mass and date of beginning of the breeding period of Brown skuas (*Stercorarius antarcticus lombergi*) in King George Island, Antarctica

between birds that lost their eggs during the In stage and those that succeeded to hatch chicks ($Z=1.53, P=0.12$).

Because of the high occurrence of nesting failure the number of birds sampled at each stage decreased severely, and 5 birds for which the technique did not get to determine the sex were excluded from the body mass analysis (S: $n=33$, In: $n=30$, Er: $n=15$, Lr: $n=10$). Females were heavier than males during the entire breeding period (est = - 123.5, $t=-3.35, P<0.01$), and, in both years, heavier females tended to pair with heavier males despite the Pearson's correlation was significant only for the first season (2012/13: $r^2=0.48, P=0.04$; 2013/14: $r^2=0.18, P=0.11$) (Fig. 2). The body mass at the In stage was not different between those birds that lost their nest during the In stage and those that succeeded to hatch chicks neither for males ($t=0.70, P=0.51$) nor females ($t=-0.22, P=0.83$) (Fig. 3). None of the blood parameters was related to the probability of incubation success.

Females experienced a loss of body mass with a slight recovery towards the last stage (In: est = - 60.65, $t=-2.27, P=0.01$; Er: est = - 90.36, $t=-3.06, P<0.01$; Lr: est = - 85.81, $t=-2.55, P=0.02$), whereas males experienced a slighter and less significant loss of body mass (In: est = - 16.62, $t=-0.63, P=0.54$; Er: est = - 72.83, $t=-2.13, P=0.04$; Lr: est = - 61.64, $t=-1.65, P=0.11$) (Table 1).

Hematological parameters

The sex of the bird and the stage of the breeding period did not interact for any of the analysed hematological parameters and none was affected by the sex. Therefore, both sexes were pooled and non-sexed birds were included (In: $n=34$, Er: $n=16$, Lr: $n=8$).

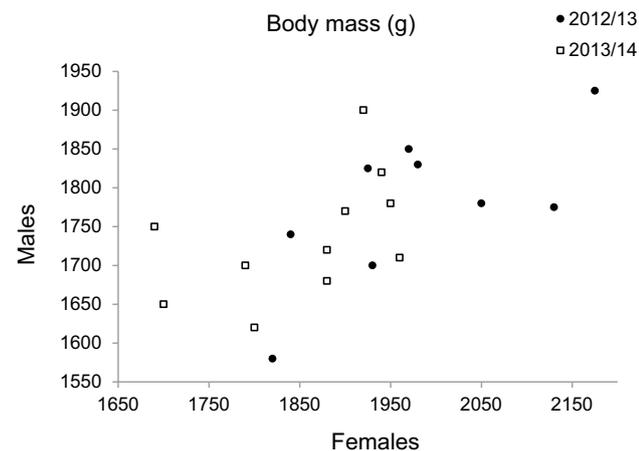


Fig. 2 Relationship of body mass between pairing males and females of Brown skuas (*Stercorarius antarcticus lonnbergi*) at the beginning of their breeding period in Potter Peninsula

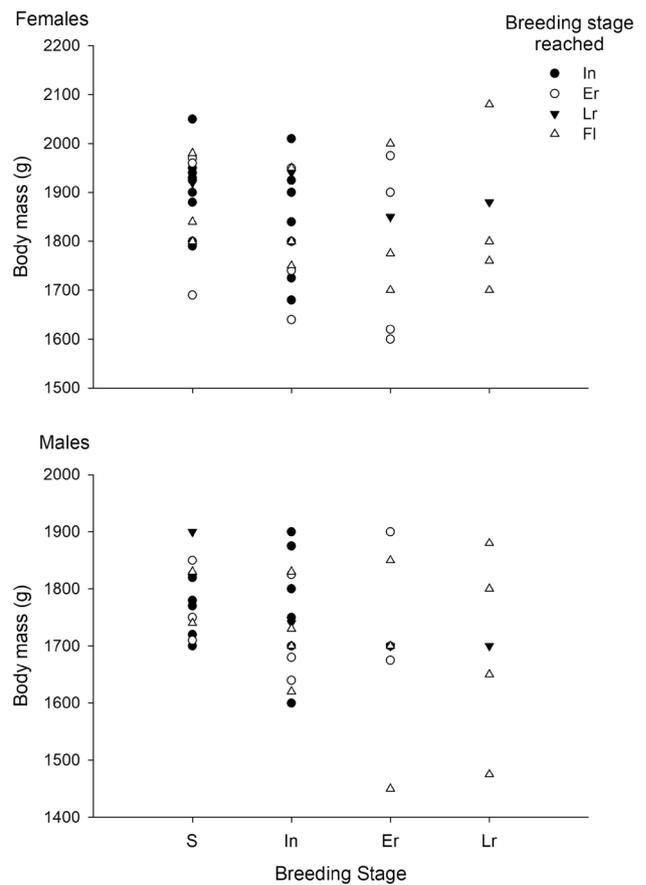


Fig. 3 Body mass of males and females of Brown skuas (*Stercorarius antarcticus lonnbergi*) that succeeded or that failed the breeding attempt at different stages of the breeding period. S beginning of the breeding period, In incubation, Er early rearing, Lr late rearing, Fl chick completely feathered surviving

The content of total proteins decreased (Er: est = - 0.39, $t=-2.42, P=0.02$; Lr: est = - 0.54, $t=-2.62, P=0.01$) and that of urea increased (Er: est = 2.23, $t=3.59, P<0.01$; Lr: est = 2.05, $t=2.55, P=0.01$) through the breeding period, whereas the concentration of uric acid did not change among stages (Er: est = 89.54, $t=0.96, P=0.34$; Lr: est = - 105.03, $t=-0.86, P=0.39$) (Fig. 3).

Table 1 Body mass (g) of males and females of Brown skuas (*Stercorarius antarcticus lonnbergi*) throughout the beginning of the incubation (S) and the three stages of their breeding period: In incubation, Er early rearing, Lr late rearing

	Males	Females
S	1775 (± 77) [16]	1897 (± 88) [17]
In	1758 (± 93) [15]	1840 (± 115) [15]
Er	1696 (± 126) [7]	1803 (± 154) [8]
Lr	1701 (± 154) [5]	1844 (± 147) [5]

Data are given as mean \pm SD and sample size in squared brackets

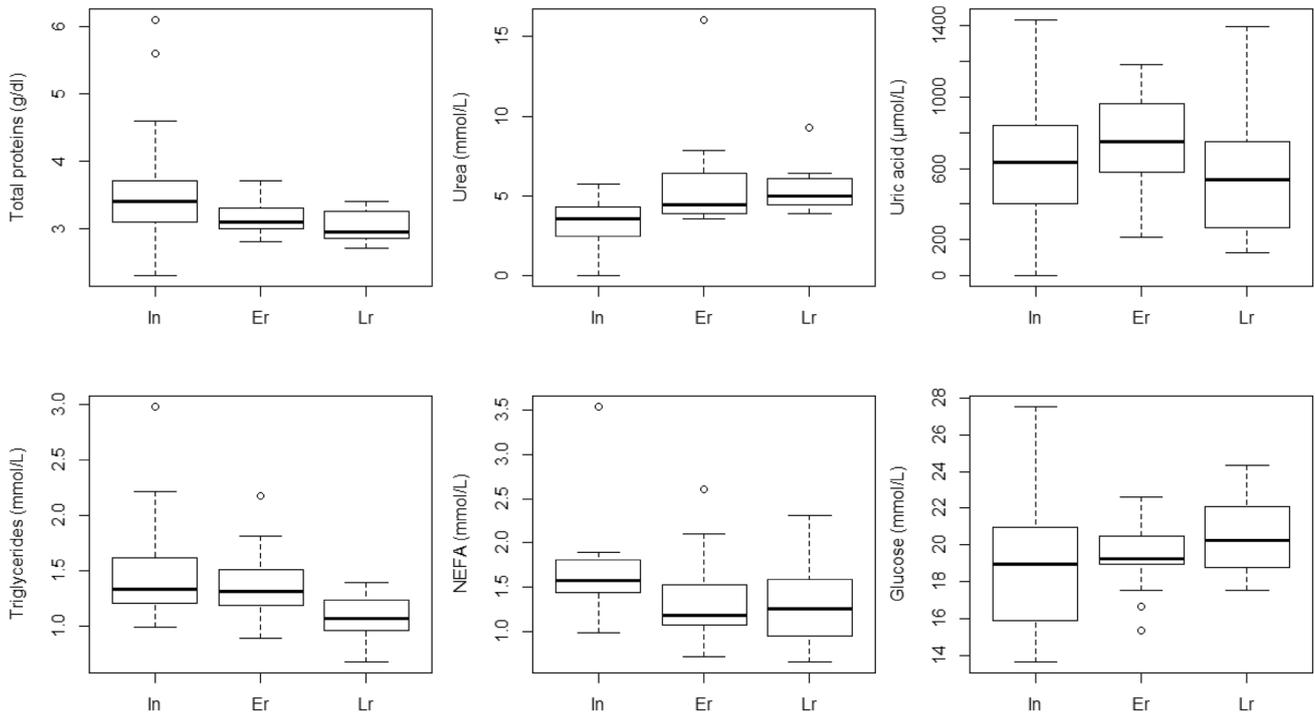


Fig. 4 Box plot indicating the changes in the concentration of hematological parameters in plasma of Brown skuas (*Stercorarius antarcticus lonnbergi*) throughout the stages of their breeding period. In:

incubation ($n=34$), Er: early rearing ($n=16$), Lr: late rearing ($n=8$) [sample size for NEFA is as follows: In: $n=10$, Er: $n=9$ and Lr: $n=8$]

The content of triglycerides decreased towards the last stage of the breeding period (Er: $est = -0.08$, $t = -0.72$, $P = 0.48$; Lr: $est = -0.37$, $t = -2.61$, $P = 0.01$) and there was a non-significant trend to a decrease of NEFA (Er: $est = -0.32$, $t = -1.11$, $P = 0.28$; Lr: $est = -0.38$, $t = -1.30$, $P = 0.21$) (Fig. 3).

Finally, the content of glucose in blood did not change among stages of the breeding period (Er: $est = 0.17$, $t = 0.19$, $P = 0.85$; Lr: $est = 1.35$, $t = 1.18$, $P = 0.24$) (Fig. 4).

Leukocyte count

In all the blood stains, there was a high predominance of heterophils and lymphocytes, with a high variability among

Table 2 Mean leucocyte count of the three breeding stages pooled for males and females of Brown skuas (*Stercorarius antarcticus lonnbergi*)

	Males ($n=23$)	Females ($n=28$)
Heterophils	68.03 (± 19.04)	56.57 (± 20.31)
Lymphocytes	17.17 (± 12.77)	31.24 (± 19.09)
Monocytes	11.86 (± 6.57)	9.62 (± 6.38)
Eosinophils	0.28 (± 0.70)	0.14 (± 0.65)
Basophils	0.28 (± 0.84)	0.05 (± 0.22)

Data are given as mean \pm SD

them and an almost complete absence of basophils (Table 2). The H:L ratio did not show changes throughout the stages of the breeding period (Er: $est = -2.44$, $t = -1.17$, $P = 0.25$; Lr: $est = -3.42$, $t = -1.45$, $P = 0.16$); however, the H:L ratio was higher in females than in males ($est = -3.74$, $t = -2.21$, $P = 0.04$) (Fig. 5).

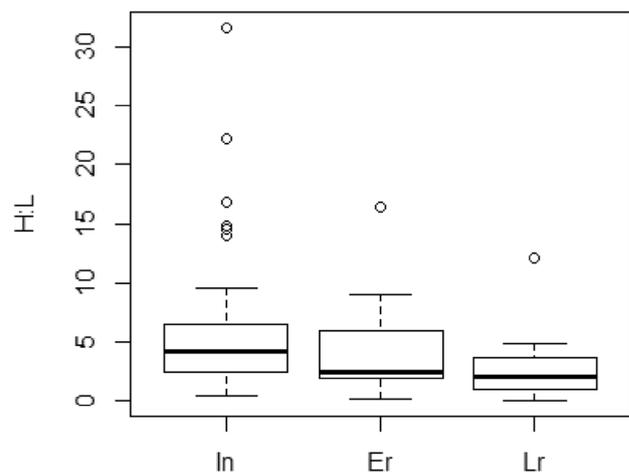


Fig. 5 Box plot showing the change in the heterophils:lymphocyte ratio (H:L) throughout the stages of the breeding period of Brown skuas (*Stercorarius antarcticus lonnbergi*). In: incubation ($n=32$), Er: early rearing ($n=15$), Lr: late rearing ($n=8$)

Discussion

Our work suggests that the low breeding success in the population studied coincides with poor and declining body condition of the breeding birds throughout their breeding period. This is evidenced by the trends found in the concentration of blood metabolites suggesting a decline in the ingestion of lipids which is not compensated with the catabolism of body fat reserves, but possibly, with the use of protein body reserves. The removal of protein stores instead of the more easily available and calorically denser fat stores suggests that this population starts the breeding period with a general low body condition without the extra availability of fat reserves to cover the energetic requirements.

The removal of protein stores from muscle is generally reflected by a low concentration in plasma of total proteins and a high concentration of the products of protein catabolism, uric acid and urea (Alonso-Alvarez et al. 2002; Ferrer et al. 2013). Contrarily, high plasma concentrations of all of these metabolites would indicate protein ingestion. Despite we did not find changes in the concentration of plasmatic uric acid, the decrease in total proteins and the increase in urea concentration throughout the breeding period suggest the use of protein stores by breeding Brown skuas (Alonso-Alvarez et al. 2002; Ferrer et al. 2013). On the other hand, the use of fat stores is indicated by a low plasma concentration of triglycerides and high concentration of NEFA (Cherel et al. 1988; Price 2010), whereas fat-store formation is reflected by high concentration of triglycerides (Smith et al. 2007; Antonio-Garcia et al. 2010; Price 2010). In the studied Brown skuas, there was a decrease in the concentration of triglycerides towards the end of the breeding season, suggesting a decrease in lipid ingestion. However, we did not find an increase in NEFA concentration—instead, we found a decreasing trend—; therefore, there is no evidence of a consumption of body fat stores during the breeding period.

Lipid reserves are used more than protein reserves as a source of energy due to their higher economy for storing and energetic content (McWilliams et al. 2004). The decrease in triglycerides concentration suggests that in the course of the breeding period the lipid intake from the diet decreases. This, added to the lack of evidence for the use of fat stores suggests that Brown skuas may already be in energetic deficit at the beginning of the breeding period and that subsequent reductions in the energy obtained from the diet would be compensated by the consumption of protein stores. The stability found in the plasma level of glucose is normal, even in fasting birds (Cherel et al. 1988), and suggests the idea that possibly protein degradation (for energy obtaining and gluconeogenesis) coupled to the glucose directly obtained from the diet allow to keep the level of energy readily available for tissues. Declines in body conditions, particularly

after chicks hatching, have been found in other bird species (Croll et al. 1991; Weimerskirch and Lys 2000). However, results indicating that protein reserves are probably being used as a source of energy, despite do not indicate that fat reserves have been completely depleted, can be compared to the condition of birds in an advanced fasting state (Cherel et al. 1988).

Body mass depends not only on lean and fat content but also on the hydric balance. Body water content has an inverse relationship with fat content (Ellis and Jehl 1991) and the use of protein reserves can be mediated by an increase in the secretion of corticosterone under stressing conditions (Hayashi et al. 1994), which also has antidiuretic effects (Holmes et al. 1983). Therefore, changes in corticosterone secretion may induce mechanisms which can explain the increase in body mass recorded towards the end of the breeding period, despite the decrease in plasma protein and triglycerides. The decrease found in total protein in plasma would be due to the decrease found in the concentration of globulins (Ibañez et al. 2018), while albumin—protein that in contrast to globulins is related to body reserves (Lumeij 1987)—increased its concentration in plasma in the last stage of the breeding period (Ibañez et al. 2018). This suggests that Brown skuas may be finishing their catabolic state towards the end of the breeding period, leading to the observed recovery of body mass.

High variability in the *H:L* ratio is common among birds (D'Amico et al. 2010; Lebigre et al. 2012). This parameter did not indicate changes in the stress level in the different stages of the breeding period of Brown skuas. However, a decrease in γ -globulin and IgY indicated a decline in the immunological conditions of these same birds throughout their breeding period (Ibañez et al. 2018), probably related to the effort experienced by Brown skuas during their breeding period. This difference in results may indicate that the leucocyte proportion is more resistant to show the effects of an immunological decline than other portions of the immune system. However, the immunological condition is poorer in females than in males, which can be related to a higher investment in breeding, which is not reflected in other body parameters.

In contrast to previous findings (Phillips et al. 2002), in the studied population of Brown skuas, heavier females tended to breed with heavier males. But in the same way than a close population (Carneiro et al. 2015), the studied one did not show a relationship between the body mass of males or females and the hatching success probability. The fixed inversion hypothesis predicts that long-lived birds would maintain their physiological conditions fixed by passing on the excessive breeding costs to their partners or their offspring, minimising on themselves the impact of, for instance, reduced food availability or accessibility (Croll et al. 1991; Gauthier-Clerc et al. 2001). It is possible that

Brown skuas started their breeding activities, after migration, in a body condition close to a minimum tolerable limit. This poor initial condition added to the need for the stocking of fat stores ready to be used in the following outbound migration (Cherel et al. 1988; Price 2010; Mitchell et al. 2012) may determine that parents prioritise their own energetic recovery and the abandonment of the offspring if the inversion in rearing chicks leads them to an even greater body condition decline. Such prioritisation of the parents' body conditions recovery preparing for the next migration is suggested in our results by the increase in body mass in the last stage of the breeding period.

That general poor body condition can explain the death of almost totally feathered chicks, without evidence of either injuries nor strong climatic events, as well as the low number of breeding attempts and hatching success in this population (Graña Grilli 2014), which is repeated in recent years in another close location (Krietsch et al. 2016). This situation indicates changing conditions from those reported in previous studies for the same area, as not only a much smaller number of Brown skuas bred but also South polar skuas—which before outnumbered Brown skuas—did not breed during the study period (Ritz et al. 2006; Hahn et al. 2007). In addition to higher numbers of breeding attempts, also higher breeding success was reported in the area 10 years before this study—0.17 and 0.57 in 2002/03 and 2003/04, respectively—even for birds with a lower mean body mass than that of the birds studied in this work (Ritz et al. 2006; Hahn et al. 2007).

We cannot attribute this high breeding failure to the location of nests, as most of them were inland relative to the penguin rookeries. Therefore, egg trampling by penguins walking between the nest and the sea cannot be the cause of the high nest failure at the incubation stage as found in other skuas populations (Hagelin and Miller 1997). Our results failed also in finding a relationship between laying date and breeding success as previous work did (Pezzo et al. 2001). In the same way, we did not find a pattern of higher breeding failure in nests farther away from penguin colonies (Pezzo et al. 2001). However, a general shortage on food resources, poor body condition, or both, may induce longer foraging time reducing nest attendance and, therefore, increasing nest predation, probably even intraspecific predation. This situation may be caused by a low amount or quality of food in either the breeding or the wintering sites that this top predator is not able to overcome. It is important to study whether this situation is also taking place at other breeding sites, in other species breeding in the same region, and its progression over the time, in order to analyse its causes and to take actions at the species or the ecosystem level.

Acknowledgements This work was made possible thanks to the logistic and financial support of Instituto Antártico Argentino. We thank D. Podestá, F. Di Sallo, L. Pagano and E. Depino for their help in the fieldwork and J. Origlia for his training in leucocyte identification. We thank P. Plaza and two reviewers for their comments and K. Bildstein for improving the English.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights The permit to carry out the fieldwork for this work was given by Dirección Nacional del Antártico. All applicable international, national, and institutional guidelines for sampling, care and experimental use of animals for the study were followed.

References

- Alonso-Alvarez C, Ferrer M, Velando A (2002) The plasmatic index of body condition in Yellow-legged Gulls *Larus cachinnans*: a food-controlled experiment. *Ibis* 144:147–149
- Antonio-Garcia MT, Hermosa Y, Aguirre JI (2010) Does breeding status influence haematology and blood biochemistry of yellow-legged gulls? *Acta Biol Hung* 61:391–400
- Boersma D, Ryder JP (1983) Reproductive performance and body condition of earlier and later nesting Ring-billed Gulls. *J Field Ornithol* 54:374–380
- Campbell T (1994) Hematology. *Avian medicine: principles and application*. Wingers, Lake Worth, pp 176–198
- Carneiro APB, Manica A, Trivelpiece WZ, Phillips RA (2015) Flexibility in foraging strategies of Brown Skuas in response to local and seasonal dietary constraints. *J Ornithol* 156:625–633
- Carrascal LM, Senar JC, Mozetich I, Uribe F, Domenech J (1998) Interactions among environmental stress, body condition, nutritional status, and dominance in great tits. *Auk* 115:727–738
- Chaurand T, Weimerskirch H (1994) Incubation routine, body mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*. *Ibis* 136:285–290
- Cherel Y, Le Maho Y (1985) Five months of fasting in king penguin chicks: body mass loss and fuel metabolism. *Am J Physiol* 18:R387–R392
- Cherel Y, Robin J-P, Maho YL (1988) Physiology and biochemistry of long-term fasting in birds. *Can J Zool* 66:159–166
- Cirule D, Krama T, Vrublevska J, Rantala MJ, Krams I (2012) A rapid effect of handling on counts of white blood cells in a wintering passerine bird: a more practical measure of stress? *J Ornithol* 153:161–166
- Croll DA, Gaston AJ, Noble DG (1991) Adaptive loss of mass in thick-billed murre. *Condor* 93:496–502
- D'Amico VL, Bertellotti M, Baker AJ, González PM (2010) Hematologic and plasma biochemistry values for endangered red knots (*Calidris canutus rufa*) at wintering and migratory sites in Argentina. *J Wildl Dis* 46:644–648
- Davies AK, Maney DL, Maerz DL (2008) The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. *Func Ecol* 22:760–772
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in Avian breeding. *Ardea* 68:225–252
- Ellis HI, Jehl JR Jr (1991) Total body water and body composition in phalaropes and other birds. *Physiol Zool* 64:973–984

- Ferrer M, Belliure J, Vinuela J, Martin B (2013) Parental physiological condition and reproductive success in chinstrap penguins (*Pygoscelis antarctica*). *Polar Biol* 36:529–535
- Gauthier-Clerc M, Le Maho Y, Gender J-P, Durant J, Handrich Y (2001) State-dependent decisions in long-term fasting king penguins, *Aptenodytes patagonicus*, during courtship and incubation. *Anim Behav* 62:661–669
- Graña Grilli M (2014) Decline in numbers of Antarctic skuas breeding at Potter Peninsula, King George Island, Antarctica. *Mar Ornithol* 42:161–162
- Griffiths R, Double MC, Orr K, Dawson RJ (1998) A DNA test to sex most birds. *Mol Ecol* 7:1071–1075
- Groscolas R, Lacroix A, Robin J-P (2008) Spontaneous egg or chick abandonment in energy-depleted king penguins: a role for corticosterone and prolactin? *Horm Behav* 53:51–60
- Guglielmo CG, Cerasale DJ, Eldermire C (2005) A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. *Physiol Biochem Zool* 78:116–125
- Gustafsson L, Nordling D, Andersson MS, Sheldon BC, Qvarnstrom A (1994) Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philos Trans R Soc Lond B Biol Sci* 346:323–331
- Hagelin JC, Miller GD (1997) Nest-site selection in south polar skuas: balancing nest safety and access to resources. *Auk* 114:638–645
- 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
- Harding AM, Welcker J, Steen H, Hamer KC, Kitaysky AS, Fort J, Talbot SL, Cornick LA, Karnovsky NJ, Gabrielsen GW et al (2011) Adverse foraging conditions may impact body mass and survival of a high Arctic seabird. *Oecologia* 167:49–59
- Harvey S, Phillips JG, Rees A, Hall TR (1984) Stress and adrenal function. *J Exp Zool* 232:633–645
- Hayashi K, Nagai Y, Ohtsuka A, Tomita Y (1994) Effects of dietary corticosterone and trilostane on growth and skeletal muscle protein turnover in broiler cockerels. *Br Poult Sci* 35:789–798
- Hennicke JC, James DJ, Weimerskirch H (2015) Sex-Specific habitat utilization and differential breeding investments in Christmas Island Frigatebirds throughout the breeding cycle. *PLoS One* 10:e0129437
- Holmes WN, Wrights A, Gorsline J (1983) Effects of aldosterone and corticosterone on cloacal water and electrolyte excretion of constantly-loaded intact and colostomized ducks (*Anas platyrhynchos*). *Comp Biochem Physiol* 74:795–805
- Ibañez A, Graña Grilli M, Figueroa A, Pari M, Montalti D (2018) Declining health status of Brown Skua (*Stercorarius antarcticus lonnbergi*) parents and their offspring during chick development. *Polar Biol* 41:193–200
- Kalmbach E, Griffiths R, Crane JE, Furness RW (2004) Effects of experimentally increased egg production on female body condition and laying dates in the great skua *Stercorarius skua*. *J Avian Biol* 35:501–514
- Klaassen M, Abraham KF, Jefferies RL, Vrtiska M (2006) Factors affecting the site of investment, and the reliance on savings for arctic breeders: the capital–income dichotomy revisited. *Ardea* 94:371–384
- Krietsch J, Esefeld J, Braun C, Lisovski S, Peter H-U (2016) Long-term dataset reveals declines in breeding success and high fluctuations in the number of breeding pairs in two skua species breeding on King George Island. *Polar Biol* 39:573–582
- Krietsch J, Hahn S, Kopp M, Phillips RA, Peter H-U, Lisovski S (2017) Consistent variation in individual migration strategies of brown skuas. *Mar Ecol Prog Ser* 578:213–225
- Kulaszewicz I, Wojczulanis-Jakubas K, Jakubas D (2017) Trade-offs between reproduction and self-maintenance (immune function and body mass) in a small seabird, the little auk. *J Avian Biol* 48:371–379
- Lebigre C, Alatalo RV, Kilpimaa J, Staszewski V, Siitari H (2012) Leucocyte counts variation and measures of male fitness in the lekking Black Grouse. *J Ornithol* 153:95–102
- Lumeij JT (1987) The diagnostic value of plasma proteins and non-protein nitrogen substances in birds. *Vet Q* 9:262–268
- Lyons JE, Collazo JA, Guglielmo CG (2008) Plasma metabolites and migration physiology of semipalmated sandpipers: refueling performance at five latitudes. *Oecologia* 155:417–427
- Machado-Filho RA, Balsamão GM, Marini MÂ (2010) Seasonal differences in immune profiles and body conditions of migratory and permanent resident neotropical flycatchers. *Condor* 112:579–590
- Marra PP, Holberton RL (1998) Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116:284–292
- Masello JF, Quillfeldt P (2004) Are haematological parameters related to body condition, ornamentation and breeding success in wild burrowing parrots *Cyanoliseus patagonus*? *J Avian Biol* 35:445–454
- McWilliams SR, Guglielmo C, Pierce B, Klaassen M (2004) Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *J Avian Biol* 35:377–393
- Minias P (2014) High glucose concentrations are associated with symptoms of mild anaemia in Whiskered Terns: consequences for assessing physiological quality in birds. *J Ornithol* 155:1067–1070
- Mitchell GW, Wheelwright NT, Guglielmo CG, Norriss DR (2012) Short-and long-term costs of reproduction in a migratory songbird. *Ibis* 154:325–337
- Moreno-Rueda G (2011) Trade-off between immune response and body mass in wintering house sparrows (*Passer domesticus*). *Ecol Res* 26:943–947
- Murphy ME (1996) Nutrition and metabolism. Avian energetics and nutritional ecology. Chapman & Hall, New York, pp 31–60
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci* 105:19052–19059
- Norris K, Evans MR (2000) Ecological immunology: life history trade-offs and immune defense in birds. *Behav Ecol* 11:19–26
- Ouyang JQ, Sharp PJ, Dawson A, Quetting M, Hau M (2011) Hormone levels predict individual differences in reproductive success in a passerine bird. *Proc R Soc Lond B Biol Sci* 278:2537–2545
- Pezzo F, Olmastroni S, Corsolini S, Forcadi S (2001) Factors affecting the breeding success of south polar skuas *Catharacta maccormicki* at Edmonson Point, Victoria Land, Antarctica. *Polar Biol* 24:389–393
- Phillips RA, Dawson DA, Ross DJ (2002) Mating patterns and reversed size dimorphism in Southern Skuas (*Stercorarius skua lonnbergi*). *Auk* 119:858–863
- Price ER (2010) Dietary lipid composition and avian migratory flight performance: development of a theoretical framework for avian fat storage. *Comp Biochem Physiol A Mol Integr Physiol* 157:297–309
- R Core Team (2014) R: A language and environment for statistical computing. Austria, Vienna
- Rae LF, Mitchell GW, Mauck RA, Guglielmo CG, Norris DR (2009) Radio transmitters do not affect the body condition of Savannah Sparrows during the fall premigratory period. *J Field Ornithol* 80:419–426
- Ritz MS, Hahn S, Janicke T, Peter H-U (2006) Hybridisation between South polar skua (*Catharacta maccormicki*) and Brown skua (*C. antarctica lonnbergi*) in the Antarctic Peninsula region. *Polar Biol* 29:253–259

- Seewagen CL, Sheppard CD, Slayton EJ, Guglielmo CG (2011) Plasma metabolites and mass changes of migratory landbirds indicate adequate stopover refueling in a heavily urbanized landscape. *Condor* 113:284–297
- Selman RG, Houston DC (1996) The effect of prebreeding diet on reproductive output in zebra finches. *Proc R Soc Lond B Biol Sci* 263:1585–1588
- Smith SB, McWilliams SR, Guglielmo CG (2007) Effect of diet composition on plasma metabolite profiles in a migratory songbird. *Condor* 109:48–58
- Stephens PA, Boyd IL, McNamara JM, Houston AI (2009) Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* 90:2057–2067
- Tveraa T, Saether B-E, Aanes R, Erikstad KE (1998) Body mass and parental decisions in the Antarctic petrel *Thalassoica antarctica*: how long should the parents guard the chick? *Behav Ecol Sociobiol* 43:73–79
- Weimerskirch H (1990) Weight loss of Antarctic Fulmars *Fulmarus glacialis* during incubation and chick brooding. *Ibis* 132:68–77
- Weimerskirch H, Lys P (2000) Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biol* 23:733–744
- Weimerskirch H, Prince PA, Zimmermann L (2000) Chick provisioning by the Yellow-nosed Albatross *Diomedea chlororhynchos*: response of foraging effort to experimentally increased costs and demands. *Ibis* 142:103–110
- Weimerskirch H, Le Corre M, Gadenne H, Pinaud D, Kato A, Ropert-Coudert Y, Bost C-A (2009) Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. *Oecologia* 161:637–649
- Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am Nat* 100:687–690