Feather Corticosterone Levels on Wintering Grounds Have No Carry-Over Effects on Breeding among Three Populations of Great Skuas (Stercorarius skua)

Sophie Bourgeon1,2, Eliza H. K. Leat3, Ellen Magnúsdóttir4, Robert W. Furness3, Hallvard Strøm2, Aævar Petersen4, Geir W. Gabrielsen2, Sveinn Are Hanssen1, Jan Ove Bustnes1

1 Norwegian Institute for Nature Research, Fram Centre, Tromsø, Norway, 2 Norwegian Polar Institute, Fram Centre, Tromsø, Norway, 3 College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, United Kingdom, 4 Iceland Institute of Natural History, Reykjavík, Iceland

Abstract

Environmental conditions encountered by migratory seabirds in their wintering areas can shape their fitness. However, the underlying physiological mechanisms remain largely unknown as birds are relatively inaccessible during winter. To assess physiological condition during this period, we measured corticosterone concentrations in winter-grown primary feathers of female great skuas (Stercorarius skua) from three breeding colonies (Bjørnøya, Iceland, Shetland) with wintering areas identified from characteristic stable isotope signatures. We subsequently compared winter feather corticosterone levels between three wintering areas (Africa, Europe and America). Among females breeding in 2009, we found significant differences in feather corticosterone levels between wintering areas. Surprisingly, levels were significantly higher in Africa despite seemingly better local ecological factors (based on lower foraging effort). Moreover, contrary to our predictions, females sharing the same wintering grounds showed significant differences in feather corticosterone levels depending on their colony of origin suggesting that some skuas could be using suboptimal wintering areas. Among females wintering in Africa, Shetland females showed feather corticosterone levels on average 22% lower than Bjørnøya and Iceland females. Finally, the lack of significant relationships between winter feather corticosterone levels and any of the breeding phenology traits does not support the hypothesis of potential carry-over effects of winter feather corticosterone. Yet, the fitness consequences of elevated feather corticosterone levels remain to be determined.

Citation: Bourgeon S, Leat EHK, Magnúsdóttir E, Furness RW, Strøm H, et al. (2014) Feather Corticosterone Levels on Wintering Grounds Have No Carry-Over Effects on Breeding among Three Populations of Great Skuas (Stercorarius skua). PLOS ONE 9(6): e100439. doi:10.1371/journal.pone.0100439

Editor: Alexandre Roulin, University of Lausanne, Switzerland

Received December 4, 2013; Accepted May 28, 2014; Published June 25, 2014

Copyright: © 2014 Bourgeon et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This study was supported by the Research Council of Norway (http://www.forskningsradet.no/en/Home_page/1177315753906), grant number 184830. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* Email: sophie.bourgeon@npolar.no

Introduction

Most seabirds breeding in temperate and Arctic regions are migratory [1] and spend most of the year away from their breeding colonies [2,3]. For these species, the environmental conditions encountered on the wintering grounds have been shown to influence breeding performance, inducing profound fitness consequences [4,5]. However, the underlying physiological mechanisms are largely unknown as birds are hardly accessible during winter. Lately, there has been tremendous technological progress to determine wintering ranges of individual migratory seabirds [3,4,5,6,7]. Corticosterone (CORT), the main stress hormone in birds [8], constitutes a physiological response of birds to changes in their environment. In American redstarts (Setophaga ruticilla), plasma corticosterone concentrations assessed during the non-breeding season appeared to be useful indicators of both physiological condition and winter habitat quality [9]. Assessing corticosterone concentrations in winter-grown feathers represents an alternative technique to assess physiological state during winter [10,11], and relate it to life-history traits outside the wintering area. For example, high feather corticosterone levels on wintering areas were attributed to stressful conditions and population declines in European trans-Saharan migrant Egyptian vultures (Neophron percnopterus) [12] and were negative predictors of future survival in wild house sparrows (Passer domesticus) [13]. Although the latter studies reported negative effects of elevated feather CORT levels on survival probabilities, they did not report effects on reproduction during the next breeding season. On the other hand, corticosterone levels measured in feathers grown months prior to egg-laying were shown to be positively associated with egg mass in atlantic puffins (Fratercula arctica) [14]. While feather CORT levels assessed in puffins were measured during the course of winter, no specific winter areas were identified.

Tracking data on great skuas (Stercorarius skua) that breed in three colonies in the northeast Atlantic (i.e., Bjørnøya, Iceland and Shetland) highlighted the use of geographically distinct wintering areas, also among individuals within a single breeding colony [15]. As previously outlined [16,17], combining tracking data with stable isotope values of primary feathers successfully allowed to assign a larger sample size of untracked individuals to wintering areas [18] while avoiding any negative effect of loggers on stress levels of birds [19]. Namely, using breeding adult great skuas caught in three distinct colonies, we could determine that they...
wintered over three core areas i.e., continental shelf seas off America, Europe and Africa the previous winter [18]. None of the Shetland birds were reported to winter off America and while Bjørnøya and Iceland birds used the three wintering areas, they did so in different proportions [18]. Using the same winter grown feathers, we assessed corticosterone levels and subsequently compared individual levels between wintering area and breeding colonies. First, we predicted that feather CORT levels should vary between wintering areas reflecting different environmental conditions on the wintering grounds but should vary independently of the breeding colony subsequently used. To examine potential carry-over effects, we thereafter related corticosterone levels measured in feathers grown during winter to the breeding phenology of birds (i.e. body mass on return, egg laying date, initial clutch size, egg length and breeding success) the following breeding season. We expected that feather CORT levels should be suitable predictors of life-history traits measured during the subsequent breeding stage. However, based on the controversies previously reported [12–14], the nature of these relationships was hard to predict.

Materials and Methods

Great skuas are large top predators with a female-biased sexual size dimorphism that breed in the North-East Atlantic. To avoid gender-specific differences in physiology and/or behaviour, 94 incubating females were caught in 2009 in three different colonies: Bjørnøya, Svalbard (74°21’N, 19°05’E) (N = 33), south-east Iceland (63°57’N, 16°24’W) (N = 32) and Foula, Shetland (60°08’N, 2°05’W) (N = 29) (see Bourgeon et al. [20] for a more detailed description of the sampling areas and techniques). Nests were followed from laying throughout chick rearing with laying date being calculated using hatching dates whenever unknown. The length of the eggs was measured to 0.1 mm accuracy using dial callipers. Females were caught on their nest while incubating using remote controlled noose traps. At each capture, body mass (±0.1 g) was recorded and blood was sampled from the brachial or tarsal vein using heparinised syringes, stored on ice and centrifuged within 2 h (5000 rpm); red blood cells were frozen and stored in individual sealed plastic bags at ambient temperature and was thereafter cut straight across perpendicular to the rachis to measure $\delta^{13}$C and $\delta^{15}$N stable isotopes (unpigmented vane of the proximal part of primary 8; see Leat et al. [18]) and feather corticosterone (distal part of primary 8; see below). Since great skuas start moulding their primary feathers (from the innermost outwards) in late autumn and through the winter [2,21], primary 8 is expectedly grown around January when birds are still in the wintering areas, as indicated by the tracking data [15]. Both stable isotope and feather CORT values therefore represent those of the wintering area.

In Shetland, all procedures (i.e., remote controlled noose trapping, ringing, blood sampling and feather clipping) were carried out under licences from the Home Office [PPL 60/3835 awarded after ethical review of the protocol by The Home Office inspectorate] and the British Trust for Ornithology. In Bjørnøya, all procedures were carried out under permits from the Governor of Svalbard, Stavanger Museum and the Directorate for Nature Management. In Iceland, all procedures were carried out under the licence from the Icelandic Institute of Natural History, Reykjavík.

Table 1. Parameter estimates for type III general linear model (GLM) assessing the influence of wintering area (i.e., Africa, America and Europe) and breeding colony (i.e., Bjørnøya, Iceland and Shetland) on feather corticosterone levels of breeding great skua (Stercorarius skua).

| Parameter estimates | Value | s.e. | t value | p value | 95% confidence interval |
|---------------------|-------|------|---------|---------|------------------------|
| Intercept           | 33.72 | 3.90 | 8.65    | <0.0001 | 25.97 - 41.47          |
| Colony (Iceland)    | –1.31 | 4.97 | –0.26   | 0.79    | –11.19 - 8.57          |
| Colony (Shetland)   | –7.91 | 4.44 | –1.78   | 0.08    | –16.72 - 0.91          |
| Winter (America)    | –10.09| 4.59 | –2.20   | 0.03    | –19.21 - 0.97          |
| Winter (Europe)     | –12.56| 4.50 | –2.79   | <0.01   | –21.51 - 3.61          |
| Colony (Iceland) x Winter (America) | –1.39 | 5.94 | –0.23   | 0.82    | –13.20 - 10.42         |
| Colony (Shetland) x Winter (America) | NA    | NA   | NA      | NA      | NA                     |
| Colony (Iceland) x Winter (Europe) | 4.40  | 6.27 | 0.70    | 0.48    | –8.05 - 16.86          |
| Colony (Shetland) x Winter (Europe) | 18.66 | 5.57 | 3.35    | <0.01   | 7.58 - 29.74           |

Parameter estimate values are given for the following factors: Colony: Bjørnøya; Winter: Africa. Numbers in bold indicate significant p-values (p<0.05). NA, not applicable; s.e., standard error.

DOI:10.1371/journal.pone.0100439.t001
Birds from Shetland wintered in Europe or Africa (12 and 17 out of 29, respectively).

Feather corticosterone was measured using the distal 15 cm of the eighth primary and expressed in pg/mm of feather. Corticosterone was first extracted using a methanol-based extraction technique as reported by Bortolotti et al. [10]. Extracts were reconstituted in saline buffer, frozen at -20°C until subsequently assayed for corticosterone using an enzyme immunoassay kit (900-097, Assay Designs Inc., USA). We validated the use of this assay with feather samples by showing parallelism of serial dilutions of feather extracts (displacement curves) and the standard curve suggesting the absence of interfering substances in methanol extracts. The cross-reactivity of the assay is high with corticosterone (100%) but low with related steroids (e.g., progesterone: 1.7%; cortisol: 0.046%; 17α-estradiol: <0.03%). Feather extracts were measured in duplicate in 4 separate plates (using the same reagents) with intra- and inter-assay variability of 9.3% (N = 16) and 13.3% (N = 6), respectively. The concentration of corticosterone in feather samples was calculated by using a standard curve run on each plate.

b. Statistical analyses

Statistical analyses were conducted using R version 2.15.2 [23]. Values are presented as means ± standard error (SE). Since feather corticosterone concentrations and all the reproductive phenology traits were normally distributed (Kolmogorov-Smirnov test, p>0.05), parametric tests were used. Type III general linear models (GLM) were first used to test for the effects of breeding colony (Bjørnøya, Iceland or Shetland) and wintering area (Africa, America or Europe) on the breeding performance the following year (Clutch size, A- and B-egg lengths and fledging success). Analyses of covariance (GLM) were subsequently used to assess the relationships between life-history traits (dependent variables) and feather CORT (independent variable) using breeding colony as a qualitative independent variable. The interaction between both predictors (i.e., feather CORT and colony) was omitted since none of the interactions were significant for any of the life-history traits (p>0.50 in all cases; data not shown). Data can be made freely available upon request.

Results

While there was no effect of breeding colony (GLM, F2,29 = 2.48, p = 0.09), wintering area significantly influenced feather CORT (GLM, F2,29 = 3.92, p = 0.02) which was significantly higher in Africa compared to America (28.89 ± 1.75 pg/mm versus 22.14 ± 1.65, respectively; Tukey’s HSD post hoc test, p = 0.02), Europe being intermediate at 25.55 ± 1.55 pg/mm (Tukey’s HSD post hoc tests: Europe/America: p = 0.31; Europe/Africa: p = 0.32). Nevertheless, as indicated by the significant interaction between breeding colony and winter area (GLM, F3,96 = 5.15, p = 0.002), feather CORT did not vary consistently among colonies; Shetland birds that spent the winter in Africa showed the lowest feather CORT levels while birds from Iceland and Bjørnøya exhibited their highest levels whenever wintering in Africa compared to other areas (Table 1; Figure 1).

We subsequently calculated two-way GLMs for each of the life-history traits (Table 2). There were no significant interactions between breeding colony and winter area for any of the traits tested (GLM, p>0.15; Table 2). While none of these traits were significantly influenced by the wintering area, four out of six significantly differed between colonies (Table 2). Thereafter, we ran analyses of covariance between each of the life-history traits and feather CORT using colony as a qualitative independent variable and found no significant relationship between feather CORT and any of the parameters (Table 3). These results suggest that winter feather CORT is not a good predictor for any of the breeding phenology traits assessed the following reproductive season.

Discussion

In migrating species, carry-over effects are described as the influences of environmental conditions encountered outside the breeding areas on the breeding performance the following year and/or fitness of individuals [4,5,24]. Nevertheless, the underlying physiological mechanisms remain unclear. It is believed that corticosterone is deposited into feathers as they grow [10], so assessing corticosterone in primary feathers collected on breeding birds likely represents corticosterone levels experienced during the previous winter. Among females breeding in 2009, we found significant differences in feather corticosterone levels between wintering areas frequented the previous winter. Namely, we found that feather CORT was significantly higher in birds wintering in...
Table 2. Influence of breeding colony (i.e., Bjørnøya, Iceland and Shetland) and wintering area (i.e., Africa, America and Europe) on reproductive phenology traits of breeding female great skuas (*Stercorarius skua*).

| Colony x Winter | N | Winter Colony | N | Winter Colony | N | Winter Colony | N | Dependent variables | F value | p value | F value | p value | F value | p value |
|-----------------|---|---------------|---|---------------|---|---------------|---|---------------------|---------|----------|---------|----------|---------|----------|
| Bjørnøya Iceland | 33 | 1433.48 | 6 | 11.33 | 1460.75 | 6 | 18.68 | 1416.15 | 14.19 | 0.09 | 0.92 | 1.78 | 0.17 | 0.10 | 0.96 |
| Shetland Iceland | 29 | 6 | 0.86 | 1 | 45.93 | 6 | 1.17 | 45.05 | 0.00 | 0.0001 | 3.17 | 0.05 | 1.80 | 0.19 | 1.80 | 0.16 |
| Europe | 32 | 1.57 | 6 | 0.09 | 2.00 | 6 | 0.00 | 1.93 | 0.05 | 0.05 | 2.16 | 0.12 | 1.61 | 0.05 | 1.32 | 0.27 |
| Africa | 30 | 68.52 | 6 | 0.56 | 71.07 | 6 | 0.50 | 68.69 | 0.04 | 0.001 | 0.54 | 0.06 | 69.87 | 0.41 | 5.92 | 0.06 |
| America | 28 | 67.13 | 6 | 0.06 | 71.07 | 6 | 0.06 | 69.87 | 0.06 | 0.06 | 5.92 | 0.04 | 69.87 | 0.41 | 5.92 | 0.06 |

The F- and p-values were calculated using type III general linear models (GLM). Numbers in bold indicate significant p-values (p < 0.05). Values (means ± standard errors) are reported for the different breeding colonies. For each row reporting significant differences between colonies, lowercase letters (a–c) indicate a significant difference in means (Tukey's HSD post hoc tests). doi:10.1371/journal.pone.0100439.t002

...
Table 3. F-, p-values and parameter estimates for the analyses of covariance between life-history traits (dependent variables) of breeding female great skuas (*Stercorarius skua*) and winter feather corticosterone levels (pg/mm) and breeding colony (i.e., Bjørnøya, Iceland and Shetland) used as independent variables (additive model excluding the interaction).

| INDEPENDENT VARIABLES | Feather corticosterone | Colony | Parameter estimates |
|------------------------|-------------------------|--------|---------------------|
|                        | F value  | p value | F value  | p value | Value  | s.e.  | t value | p value |
| 1/Body mass (g)        | 1.43     | 0.24    | 2.48     | 0.09    | Intercept | 1406.76 | 26.65 | 52.79  | <0.0001 |
|                        |          |         |          |         | Feather corticosterone | 1.11 | 0.93 | 1.20 | 0.24 |
|                        |          |         |          |         | Colony (Iceland) | 26.60 | 20.66 | 1.29 | 0.20 |
|                        |          |         |          |         | Colony (Shetland) | -22.64 | 22.28 | -1.02 | 0.31 |
| 2/Laying date (julian date) | 0.01 | 0.93 | 147.57 | <0.0001 | Intercept | 168.55 | 1.87 | 90.09 | <0.0001 |
|                        |          |         |          |         | Feather corticosterone | 0.01 | 0.06 | 0.09 | 0.93 |
|                        |          |         |          |         | Colony (Iceland) | -24.42 | 1.49 | -16.33 | <0.0001 |
|                        |          |         |          |         | Colony (Shetland) | -19.78 | 1.52 | -13.05 | <0.0001 |
| 3/Initial clutch size (eggs) | 0.41 | 0.52 | 15.17 | <0.0001 | Intercept | 1.63 | 0.11 | 15.32 | <0.0001 |
|                        |          |         |          |         | Feather corticosterone | 0.00 | 0.00 | -0.64 | 0.52 |
|                        |          |         |          |         | Colony (Iceland) | 0.42 | 0.08 | 5.10 | <0.0001 |
|                        |          |         |          |         | Colony (Shetland) | 0.37 | 0.09 | 4.24 | <0.0001 |
| 4/A-egg length (mm)    | 3.68     | 0.06    | 9.50     | <0.0001 | Intercept | 70.19 | 1.03 | 68.12 | <0.0001 |
|                        |          |         |          |         | Feather corticosterone | -0.07 | 0.04 | -1.92 | 0.06 |
|                        |          |         |          |         | Colony (Iceland) | 3.30 | 0.80 | 4.14 | <0.0001 |
|                        |          |         |          |         | Colony (Shetland) | 2.61 | 0.83 | 3.14 | <0.01 |
| 5/B-egg length (mm)    | 2.66     | 0.11    | 12.72    | <0.0001 | Intercept | 68.36 | 0.99 | 69.34 | <0.0001 |
|                        |          |         |          |         | Feather corticosterone | -0.05 | 0.04 | -1.63 | 0.11 |
|                        |          |         |          |         | Colony (Iceland) | 4.02 | 0.81 | 4.94 | <0.0001 |
|                        |          |         |          |         | Colony (Shetland) | 1.86 | 0.85 | 2.18 | 0.03 |
| 6/Chicks fledged       | 0.10     | 0.76    | 11.06    | <0.0001 | Intercept | 0.08 | 0.15 | 0.57 | 0.57 |
|                        |          |         |          |         | Feather corticosterone | 0.00 | 0.01 | 0.31 | 0.76 |
|                        |          |         |          |         | Colony (Iceland) | -0.06 | 0.11 | -0.50 | 0.62 |
|                        |          |         |          |         | Colony (Shetland) | 0.46 | 0.12 | 3.89 | <0.0001 |

Parameter estimate values are given for the following factor: Colony: Bjørnøya. Numbers in bold indicate significant p-values (p < 0.05). s.e., standard error.
following breeding season. In black-legged kittiwakes (Rissa tridactyla), it was shown that the outcome of the breeding event (i.e., failure or success) influenced the date and place of migration while there was no evidence of any fitness difference between individuals wintering in different areas [34]. Since skuas seem to consistently use the same wintering areas from year to year [6,15] regardless of the outcome of the previous breeding event, there could be a mismatch between the foraging abilities or physiological adaptations of the birds and the wintering areas further supporting the hypothesis that some skuas might use suboptimal wintering areas. Likewise, Eurasian spoonbills (Platalea leucorodia leucorodia) were shown to migrate to suboptimal wintering sites offering lower fitness prospects [35]. Winter feather corticosterone might therefore not be a good predictor of future breeding success in great skuas. Whether higher corticosterone concentrations during winter might have long-term effects on survival remain nonetheless unknown and future studies should investigate the matter.

References

1. Gaston AJ (2004) Seabirds: A Natural History. T & AD Poyser, London.
2. Furness RW (1987) The Skuas. T & A D Poyser, Calton.
3. Egevang C, Sterhouse IJ, Phillips RA, Petersen A, Fox JW, et al. (2010) Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. Proc Natl Acad Sci USA 107: 2070–2071.
4. Marra PP, Hobson KA, Holmes KT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282: 1884–1886.
5. Sedinger JS, Schamber JL, Ward DH, Nicolai CA, Conant B (2011) Carryover Effects Associated with Winter Location Affect Fitness, Social Status, and Population Dynamics in a Long-Distance Migrant. Am Nat 178 (3): E110–E123.
6. Phillips RA, Bearhop S, Silk JRD, Bearhop S, McGill R, et al. (2007) Movements, winter distribution and activity patterns of Falldon and brown skuas: insights from loggers and isotopes. Mar Ecol Prog Ser 354: 281–291.
7. Sterhouse IJ, Egevang C, Phillips RA (2012) Trans-equatorial migration, staging sites and wintering area of Sabine’s Gulls Larus sabini in the Atlantic Ocean. Bird 114: 42–51.
8. Wingfield JC (1994) Modulation of the adrenocortical response to stress in birds. In: Davey KG, Peter KE, Toke SS, editors. Perspectives in comparative endocrinology. National Research Council of Canada, Ottawa. pp. 520–528.
9. Marra PP, Holberton RL (1996) Corticosterone Levels as Indicators of Habitat Quality: Effects of Habitat Segregation in a Migratory Bird during the Non-Breeding Season. Oecologia 116 (1/2): 204–292.
10. Borodotti GR, Marchant TA, Blas J, German T (2008) Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. Func Ecol 22: 494–500.
11. Lattin CR, Reed JM, DesRochers DW, Romero LM (2011) Elevated corticosterone correlates with corticosterone-induced decreased feather quality: a validation study. J Avian Biol 42: 247–252.
12. Carrete M, Borodotti GR, Sánchez-Zapata JA, Delgado A, Cortés-Avizanda A, et al. (2013) Stressful conditions experienced by endangered Egyptian vultures on African wintering areas. Anim Conserv 16: 355–358.
13. Kooren J, Nakasoga S, Burke T, Soma KK, Wyne-Edwards KE, et al. (2012) Non-breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. Proc R Soc B 279: 1560–1565.
14. Koonsenberg AK, Hipfler JM, McKay DW, Storey AE (2013) Corticosterone and stable isotopes in feathers predict egg size in Atlantic Puffins Fratercula arctica. Bird 155: 413–418.
15. Magnusdottir E, Leat EHK, Bourguin S, Strom H, Petersen A, et al. (2012) Wintering areas of Great Skuas Stercorarius skua breeding in Scotland, Iceland and Norway. Bird Study 59: 1–9.
16. Phillips RA, Bearhop S, McGill RAR, Dawson DA (2009) Stable isotopes reveal longest animal migration. Proc R Soc B 276: 1809–1816.
17. Gonzalez-Solis J, Smyrli M, Militao T, Gremillet D, Tveraa T, et al. (2011) Combining stable isotope analyses and geolocation to reveal kittiwake migration. Mar Ecol Prog Ser 435: 251–274.
18. Leat EHK, Bourguin S, Magnusdottir E, Gabrielsen GW, Grecian VJ, et al. (2011) The influence of wintering area on concentration and pattern of persistent organic pollutants in a breeding migratory seabird. Mar Ecol Prog Ser 491: 277–293.
19. Quinnell P, McGill RA, Furness RW, Mostl E, Lotzynia K, et al. (2012) Impact of nature geolocation loggers on a small petrel, the thin-billed prion Pachyptila rikihiti. Mar Biol 159: 1009–1016.
20. Bourguin S, Leat EHK, Furness RW, Magnusdottir E, Fox AK, et al. (2012) Individual variation in biomarkers of health: influence of persistent organic pollutants in Great skuas (Stercorarius skua) breeding at different geographical locations. Environ Res 118: 31–39.
21. Thompson DR, Bearhop S, Speckman JR, Furness RW (1998) Feathers as a means of monitoring mercury in seabirds: insights from stable isotope analysis. Environ Pollut 101: 193–200.
22. Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing of non-raiting birds. J Avian Biol 30: 116–121.
23. R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/. Accessed 2014 May 30.
24. Sorensen MC, Hipfler JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. J Anim Ecol 78: 469–467.
25. Wingfield JC, Moore MJ, Farmer DS (1983) Endocrine Responses to Inclement Weather in Naturally Breeding Populations of White-Crowned Sparrows (Zonotrichia leucophrys gambiaca). The Am 100 (3): 56–62.
26. Kiñanyk AS, Wingfield JC, Pint JF (1999) Dynamics of Food Availability, Body Condition and Physiological Stress Response in Breeding Black-Legged Kittiwakes. Func Ecol 13 (5): 577–584.
27. Kiñanyk AS, Wingfield JC, Pint JF (2008) Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. Behav Ecol 19 (5): 619–625.
28. Angelier J, Clément-Chastel G, Gabrielsen GW, Chastel O (2007) Corticosterone and time-activity budget: An experiment with Black-legged kittiwakes. Horm Behav 52: 482–491.
29. Magnusdottir E (2012) Winter distribution and foraging activity of Great Skuas Stercorarius skua. Master’s thesis, Faculty of Life and Environmental Sciences, University of Iceland, 44 pages + viii.
30. Bourguin S, Leat EHK, Furness RW, Borgu K, Hansen SA, et al. (2013) Dietary versus maternal sources of organochlorines in top predator seabird chicks: an experimental approach. Environ Sci Technol 47: 3963–3970.
31. Råberg L, Grahn M, Häuslerquist D, Svensson E (1998) On the adaptive significance of stress-induced immunosuppression. Proc R Soc B 265: 1637–1641.
32. Costantini D, Fanfani A, Dell’Omo G (2008) Effects of corticosteroids on oxidative damage and circulating carotenoids in captive adult kestrels Falco tinnunculus. J Comp Physiol B 178: 829–835.
33. Romero LM, Strohlie D, Wingfield JC (2005) Corticosterone inhibits feather growth: potential mechanism explaining seasonal down regulation of cortico-sterone during molt. Comp Biochem Physiol A Mol Integr Physiol 141 (4): 65–73.
34. Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, et al. (2011) Seasonal interactions in the black-legged kittiwake Rissa tridactyla: links between breeding performance and winter distribution. Proc R Soc B 278: 2412–2418.
35. Lok T, Overdijk O, Timmergen JM, Piersma T (2011) The paradox of spoonbill migration: most birds travel to where survival rates are lowest. Anim Behav 82: 837–844.