

Distinct lay dates in three species of *Pygoscelis* penguin

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Introduction

The genus *Pygoscelis* contains three different species of penguin: Adelie (*Pygoscelis adeliae*), Chinstrap (*Pygoscelis antarcticus*) and Gentoo (*Pygoscelis papua*), which occur in overlapping ranges throughout the marine ecosystem of the Western Antarctic Peninsula¹. The species generally have similar life history patterns: they return to breeding sites around October, to coincide with the start of the Antarctic summer. The partners then undergo courtship, after which they lay (usually two) eggs. After incubation and finally hatching, the parents will take turns between ‘guarding’ the chick and foraging for food². While the general life history pattern between species is similar, there are also some major differences between them in terms of migration patterns, fasting behaviour and diet².

For example, Adelie penguins migrate long distances to common overwintering grounds on the ice. When they return to summer breeding grounds, they fast for three weeks during courtship and egg laying³. Gentoo penguins, on the other hand, overwinter on the near shore and forage in the sea year-round. The female fasts for just one week before egg laying³.

All three species forage in ice-free waters during the summer, but previous research has shown that they have different diets⁴. For example, Chinstrap penguins have a higher consumption of krill, while Gentoo birds also eat krill but have a higher proportion of fish in their diet. When they do eat fish, the Chinstrap diet is dominated by one pelagic species and two mesopelagic species⁴. The Gentoo fish diet is dominated by a combination of pelagic and benthic fish species⁴.

For all birds, it is important to align the food demand of the chick with food availability in the environment. Species that are better at making this alignment should have greater reproductive success³. This is particularly important for penguins, not just because they must factor in a fasting period pre-laying, but also because the Antarctic is a highly seasonal environment where food availability and weather varies greatly throughout the year⁵. It has previously been shown that penguins that delay breeding from the optimum have reduced reproductive success⁶ because of the limited time available to provision food to offspring before food resources are depleted³.

Hypothesis

Therefore, given the differences between the species in migration patterns, fasting behaviour, and diet, all of which are likely to influence trade-offs for the optimal timing of egg laying, I hypothesize that the three species will have distinct laying dates.

Methods

A 2014 study by Gorman et al studied *Pygoscelis* penguins on the Palmer Archipelago, located west of the Antarctic Peninsula, near Anvers island¹. They collected morphological data on nesting penguins to study sexual dimorphism, but at the same time they recorded the clutch initiation date (CID) of each nesting pair. This data can now be freely accessed in the ‘palmerpenguins’ package in R. The study nests were located on three different islands - Biscoe (64° 48S, 63° 46W), Torgersen (64° 46S, 64° 04W), and Dream (64°

439S, 64° 139W). The study ran for three years from 2007-2009 and in total recorded 76 Adelie nests, 34 chinstrap nests, and 62 Gentoo nests¹.

I used this dataset to examine the CID of the different species, and look at how this varies across the three years of the study. First, I converted the calendar dates into Julian dates so that 'lay date' became a continuous variable. Julian dates give each day of the year a number from 1 to 365, starting from the 1st January that year. I created some exploratory figures, and then used ANOVA to test for differences in means between species. A statistically significant result from an ANOVA does not tell us which group means are different from which other group means, and therefore I used a Tukey-Kramer test to find out which groups have significantly different means.

```
knitr::opts_chunk$set(echo = TRUE)

#load all the required packages
library(tidyverse)#for cleaning the data
library(janitor)#for cleaning the data
library(lubridate)#for manipulating dates
library(palmerpenguins)#contains the dataset
library(here)#to specify the directory
library(ggplot2)#for making plots
library(lme4)#for making linear models
library(grid)#for making multi-panel figures
library(gridExtra)#for making multi-panel figures
library(dplyr)#for manipulating the data
library(ggsignif) #for adding significance stars to plots

#load the raw data and save it
penguins_raw <- read_csv(here("data", "penguins_raw.csv"), show_col_types = FALSE)
write_csv(penguins_raw, here("data", "penguins_raw.csv"))

#clean the data and save it
source(here("functions", "cleaning.R"))
penguins_clean <- cleaning_penguins(penguins_raw)
write_csv(penguins_clean, here("data", "PenguinsClean.csv"))

#convert calendar dates into Julian dates

#save date in a date format
penguins_clean$date_egg <- as.Date(penguins_clean$date_egg, format = "%Y-%m-%d")

#convert to julian date
penguins_clean$julian_date <- as.integer(format(penguins_clean$date_egg, "%j"))

#Add a column called 'year_egg_laid'
penguins_clean$year_egg_laid <- format(penguins_clean$date_egg, "%Y")
```

Results

QUESTION 1: Creating a bad exploratory figure

```
#calculate mean lay date for the three different penguin species
mean_lay_dates <- penguins_clean %>%
```

```

group_by(species) %>%
  summarize(mean_julian_date = mean(julian_date, na.rm = TRUE))

#assign colours to the three different species
species_colours <- c("Adelie" = "darkorange",
                     "Chinstrap" = "purple",
                     "Gentoo" = "cyan4")

#make a really bad exploratory boxplot
bad_plot <- ggplot(
  data = mean_lay_dates,
  aes(
    x = factor(species),
    y = mean_julian_date,
    fill = species)) +
  geom_bar(stat = "identity") +
  scale_fill_manual(values = species_colours) +
  labs(
    x = "Species",
    y = "Mean Lay Date") +
  theme_bw()
bad_plot

```

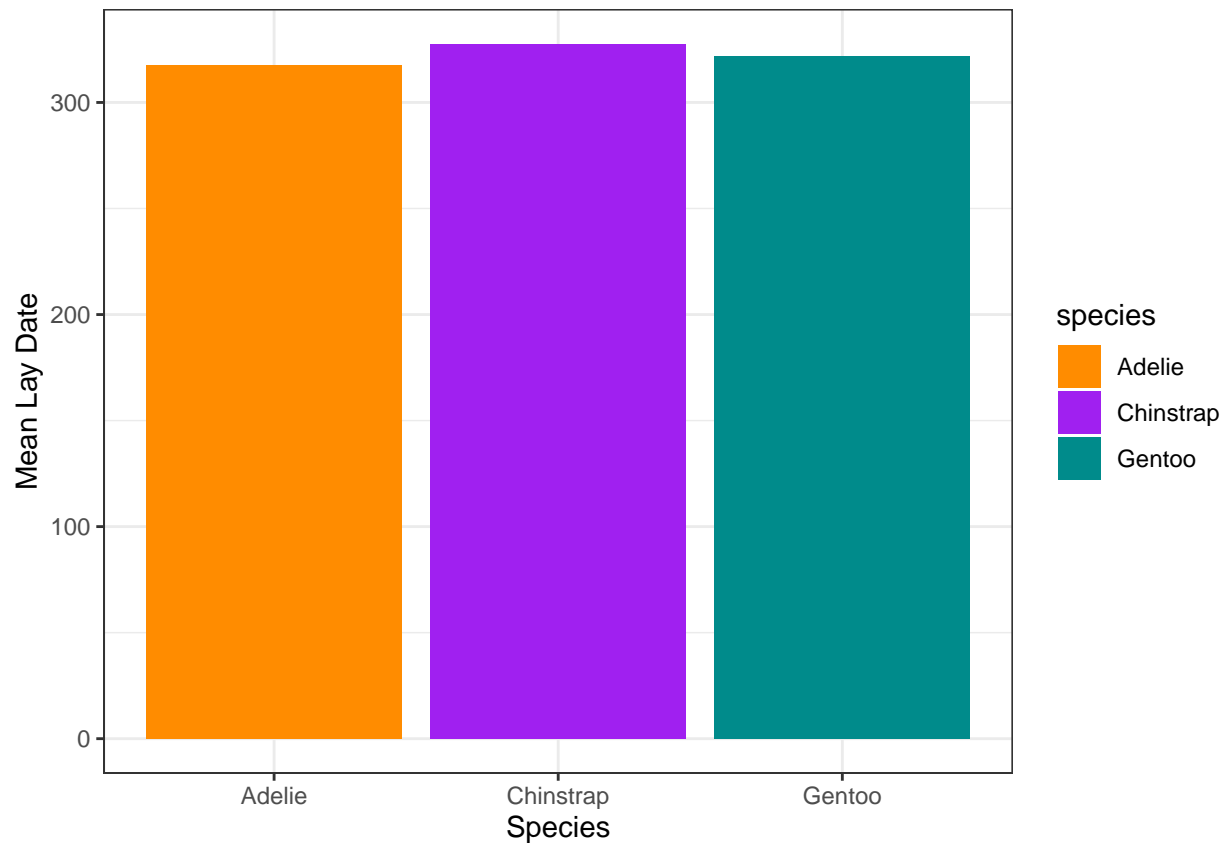


Figure 1: A boxplot of the mean lay date of the three species of Pygoscelis penguin

This Figure 1 shows the mean late day for all three different penguin species. While it is technically correct, there are number of issues with it that make it misleading:

- It does not show the raw datapoints. This means that we have no idea of the sample size in each group, and we cannot see the distribution of the data. A lot of statistical analyses assume normally distributed data, and therefore without seeing the distribution we do not know whether any subsequent statistical tests are valid.
- The scale on the y-axis is misleading, suggesting that there is very little difference in mean lay date between species. However, if we were simply to re-scale the y-axis we would see that there is in fact a 10-day difference in the mean lay date of Adelie penguins ($x = 317$) compared to Chinstrap penguins ($x = 327$).
- The bar chart does not include any error bars, and so we do not know how confident we are in these estimates of mean lay date for each species.

The Lay date of different species would be much better displayed using a boxplot and jittered data points to show the raw data, or boxplot and violin plot to show the distribution of the data. A label including the sample size for each group would also be helpful.

QUESTION 2: Creating a good exploratory figure

```
#lay date vs species
lay_date_vs_species <- ggplot(
  data = penguins_clean,
  aes(
    x = factor(species),
    y = julian_date)) +
  geom_violin(aes(fill = species),
    width = 0.4,
    alpha = 0.8,
    show.legend = FALSE) +
  geom_boxplot(aes(),
    width = 0.05,
    alpha = 1.0,
    show.legend = FALSE) +
  scale_fill_manual(values = species_colours) +
  theme_bw() +
  labs(
    x = "Species",
    y = " Julian Lay Date"
  )

#lay date in different years
lay_date_vs_year <- ggplot(
  data = penguins_clean,
  aes(
    x = year_egg_laid,
    y = julian_date)) +
  geom_violin(aes(fill = species),
    alpha = 0.8,
    position = position_dodge(0.8),
    show.legend = FALSE) +
  scale_fill_manual(values = species_colours) +
  labs(
```

```

x = "Year",
y = "Julian Lay Date") +
theme_bw()

#make a multi-panel figure
grid.arrange(lay_date_vs_species, lay_date_vs_year, ncol = 2)

grid.text("A", x = 0.07, y = 0.95, gp = gpar(fontsize = 12)) #Adds label 'A' to first graph
grid.text("B", x = 0.57, y = 0.95, gp = gpar(fontsize = 12)) #Adds label 'B' to second graph

```

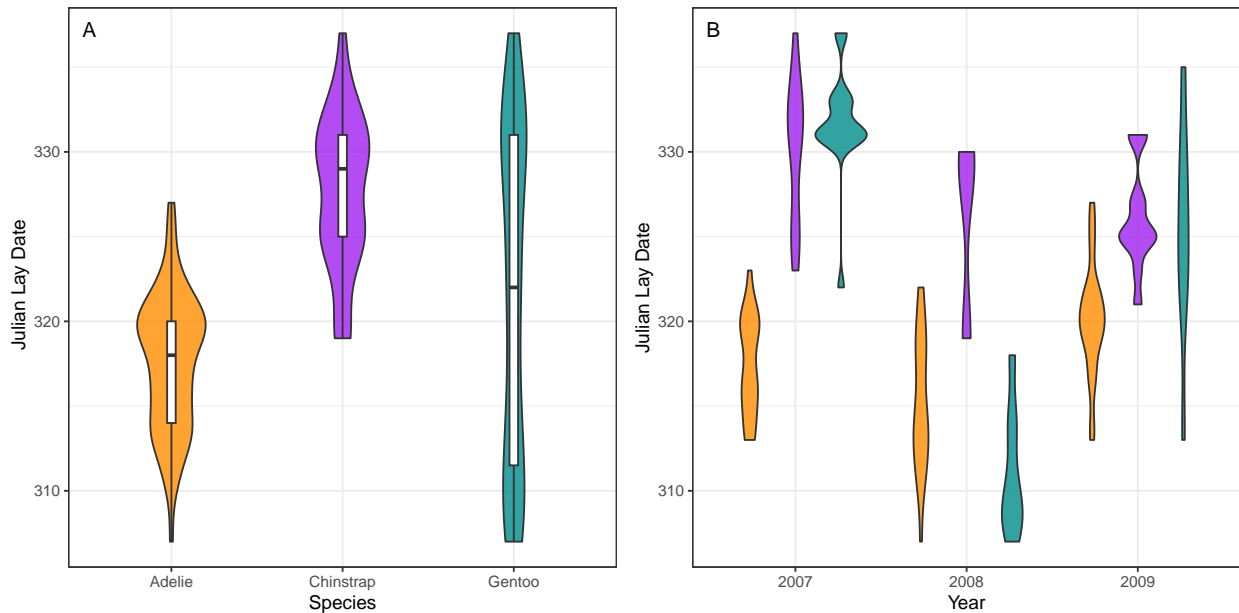


Figure 2: The distribution of lay dates for three species of *Pygoscelis* penguin. A) violin plot and boxplots of the lay date for the three species. B) Violin plot of the lay dates across the three years of the study.

We can see from figure 2.A that lay date seems to differ by species. The Adelie penguins seem to have the earliest CID, while the Chinstrap penguins seem to have a much later CID. Gentoos have a much broader distribution of CID.

The data for Adelie and Chinstrap penguins appear to be approximately normally distributed, but the Gentoo data has so much more variation that it appears to differ more from the normal distribution.

From figure 2.B we can see that across the three years of the study, the CID remained roughly consistent for Adelies and Chinstraps, but Gentoo birds showed an earlier CID in 2008 compared to the other years of the study.

Following these observations from my exploratory analysis, I ran ANOVA and Tukey-Kramer tests for two hypotheses:

- 1) That the three species have distinct lay dates from each other
- 2) That Gentoos laid significantly earlier in 2008

Statistical analysis for lay date across species

```

#ANOVA for lay date across species
date_vs_species_model <- lm(julian_date ~ species, data = penguins_clean)
anova(date_vs_species_model)

## Analysis of Variance Table
##
## Response: julian_date
##           Df Sum Sq Mean Sq F value    Pr(>F)
## species      2  4570.7  2285.35   50.015 < 2.2e-16 ***
## Residuals 321 14667.6    45.69
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

#pairwise comparisons using Tukey-Kramer test
TukeyHSD(aov(date_vs_species_model))

##      Tukey multiple comparisons of means
##      95% family-wise confidence level
##
## Fit: aov(formula = date_vs_species_model)
##
## $species
##              diff          lwr          upr    p adj
## Chinstrap-Adelie 10.000966  7.633738 12.368194 0.0e+00
## Gentoo-Adelie     4.060541  2.068174  6.052909 7.3e-06
## Gentoo-Chinstrap -5.940425 -8.375199 -3.505651 1.0e-07

#Boxplot showing the results of the Tukey-Kramer test
results_plot <- ggplot(penguins_clean,
  aes(x = species, y = julian_date)) +
  geom_boxplot(
    aes(fill = species),
    width = .25,
    alpha = .3,
    outlier.shape = NA) +
  geom_point(
    aes(color = species),
    size = 1.5,
    position = position_jitter(seed = 0, width = .1)
  ) +
  scale_color_manual(values = species_colours, guide = "none") +
  scale_fill_manual(values = species_colours, guide = "none") +
  labs(
    x = "Species",
    y = "Lay Date") +
  geom_signif(comparisons = list(c("Adelie", "Chinstrap"),
                                c("Chinstrap", "Gentoo"),
                                c("Adelie", "Gentoo")),
    annotations = c("***", "***", "***"), #adding the significance stars
    test = "aov",
    y_position = c(338, 339, 342)) +
  scale_y_continuous(limits = c(307, 345)) + #changing the scale of the y-axis

```

```
theme_bw()
results_plot
```

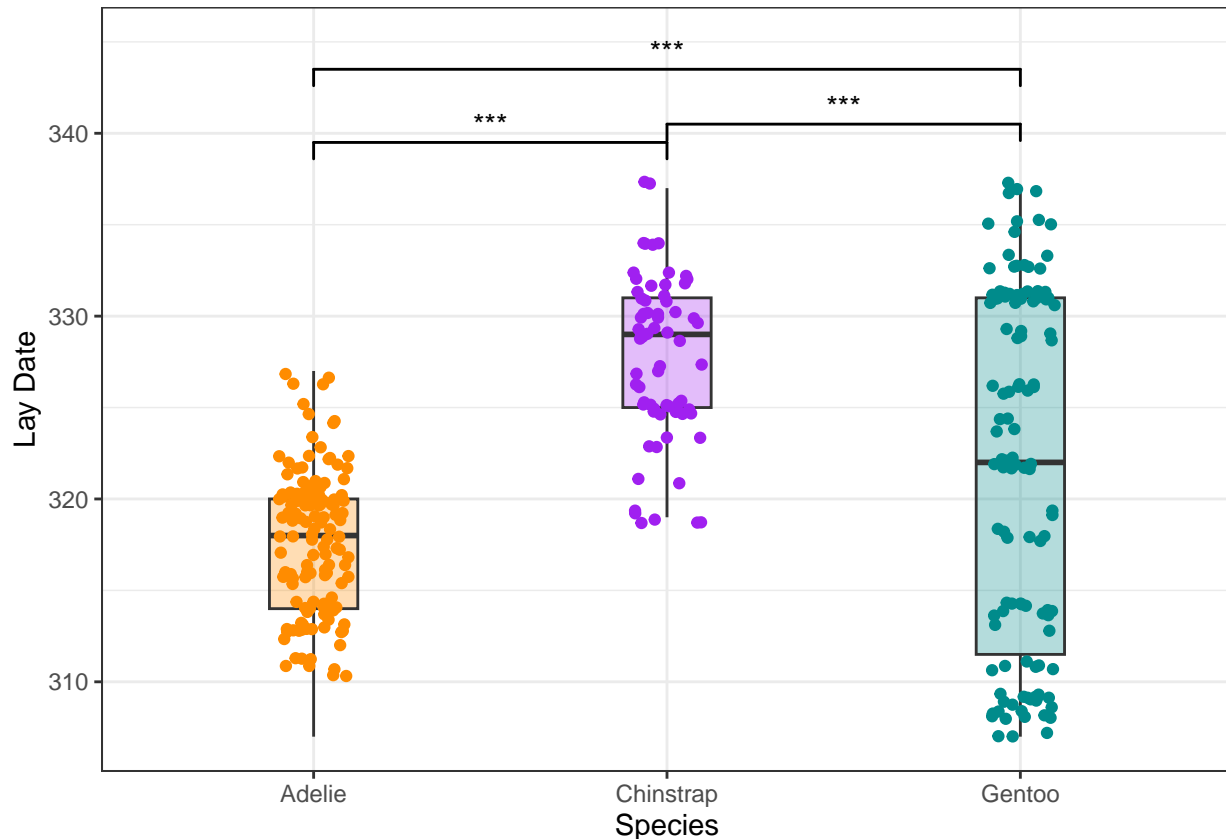


Figure 3. A boxplot showing the results of the Tukey-Kramer test. A p-value of <0.001 is shown with '***', showing that all three species had significantly distinct CID from all other species.

Statistical analysis for lay date vs year for Gentoo penguins

```
#filter the data to just look at Gentoo penguins
gentoo_birds <- penguins_clean %>%
  filter(species == "Gentoo")

#ANOVA for lay date across different years for Gentoo penguins
date_vs_year_model <- lm(julian_date ~ year_egg_laid, data = gentoo_birds)
anova(date_vs_year_model)
```

```
## Analysis of Variance Table
##
## Response: julian_date
##           Df Sum Sq Mean Sq F value    Pr(>F)
## year_egg_laid  2 8825.8  4412.9  220.88 < 2.2e-16 ***
## Residuals    115 2297.6    20.0
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
#Pairwise comparisons using Tukey-Kramer test
TukeyHSD(aov(date_vs_year_model))
```

```
##    Tukey multiple comparisons of means
##      95% family-wise confidence level
##
## Fit: aov(formula = date_vs_year_model)
##
## $year_egg_laid
##           diff           lwr           upr p adj
## 2008-2007 -20.576389 -23.030593 -18.122185 0e+00
## 2009-2007  -6.199695  -8.703157  -3.696233 1e-07
## 2009-2008  14.376694  12.085312  16.668076 0e+00
```

Discussion

Lay date vs species

We can see from figure 3 that the three species have distinct lay dates from each other. Indeed, the ANOVA gave a P-value of 2.2×10^{-16} , and the Tukey-Kramer test showed that all pairwise comparisons were significant. We already know that the timing of CID is important for penguins, because birds that delay breeding have lower reproductive success⁶. Therefore, can conclude that the different species of Pygoscelid penguin have different optimal lay dates.

Food available to feed the chick might influence the optimal lay date, and since the species have different summer diets, perhaps these differences in lay date reflect the availability of different food sources throughout the Antarctic summer. Future research could examine the chick-provisioning diet of the three species, and see whether CID is timed to correlate with maximum abundance of those food sources when the chick requires most food.

These three species have overlapping ranges and often nest together. Another possible explanation for why they have distinct lay dates could be that it is a mechanism of niche separation, allowing them to feed on different diets and therefore promote coexistence.

The different migration patterns of the birds might also influence lay date. Adelie and Chinstrap birds migrate, while Gentoos do not². This might explain why Gentoos are able to be more flexible with their CID, because they do not have to factor in time for migration, and are able to assess the local conditions and adjust their CID accordingly. Perhaps by the time Adelie and Chinstrap birds arrive at their nesting sites, they must lay eggs whether or not the local conditions are exactly ideal, because they must also factor in time for migration to and from summer breeding grounds.

Lay date vs year in Gentoo birds

The second ANOVA, looking at Gentoo lay date across the three years, gave a significant result with a P-value of 2.2×10^{-16} . The Tukey-Kramer test confirmed that all three years had distinct lay dates, but the most significant comparisons were those involving the year 2008, while the comparison 2009-2007 was less significant.

In 2014, Gorman et al reported that 2008 was the lowest sea ice season since 1979, whereas 2007 had intermediate sea ice, and 2009 had high sea ice¹. Indeed, Hinke et al reported in 2012 that Gentoo birds appear to be able to plastically adjust their lay date in response to changing temperature³. Therefore, it seems likely that Gentoos have a wider distribution of lay dates and can therefore plastically adjust their CID. 2008 was a particularly warm year, with lower sea ice, and therefore these birds laid earlier.

Antarctica is one of the most rapidly warming parts of the planet⁷. Under these changing environmental conditions, species which can plastically adjust their lay date are more likely to have greater reproductive

success and therefore higher fitness. The results of this analysis suggest that Gentoos might be more resilient to climate change than Adelie or Chinstrap penguins.

Conclusion

Overall, this analysis has produced two conclusions:

1. Different species of Pygoscelid have distinct lay dates
2. Gentoo penguins laid earlier in 2008, suggesting they might have more plasticity in their CID.

We have discussed how many biotic factors are likely to influence the optimum lay date for each species: migration, fasting, diet and competition/coexistence between species. Many abiotic factors might also be important: we have discussed how sea ice coverage and temperature might explain the earlier lay date of Gentoos in 2008, but many other abiotic factors such as rainfall and snowfall are also likely to be important in determining the optimal CID.

Future research should focus on unpicking exactly which of these biotic and abiotic factors influence lay date, and this might explain exactly why lay date differs between species. In this study, we have only been able to hypothesise that these factors might be important. A long-term dataset of CID over many years (i.e. at least 10 years) and temperature would allow a more detailed analysis such as a mixed-effects model on whether temperature affects CID, with ‘year’ as a random effect.

It is important to understand what factors affect lay date, particularly in the context of warming temperatures in the Antarctic. The limited analysis done here suggests that Gentoo birds might be more resilient to climate change than Adelie and Chinstrap penguins.

References

1. Gorman, K. B., Williams, T. D. & Fraser, W. R. Ecological sexual dimorphism and environmental variability within a community of Antarctic penguins (Genus *Pygoscelis*). *PLoS One* 9, (2014).
2. Black, C. E. A comprehensive review of the phenology of *Pygoscelis* penguins. *Polar Biology* vol. 39 405–432 Preprint at <https://doi.org/10.1007/s00300-015-1807-8> (2016).
3. Hinke, J. T., Polito, M. J., Reiss, C. S., Trivelpiece, S. G. & Trivelpiece, W. Z. Flexible reproductive timing can buffer reproductive success of *Pygoscelis* spp. penguins in the Antarctic Peninsula region. *Mar Ecol Prog Ser* 454, 91–104 (2012).
4. Polito, M. J. et al. Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins. *Mar Ecol Prog Ser* 519, 221–237 (2015).
5. Biochem, C. & Clarke, A. SEASONALITY IN THE ANTARCTIC MARINE ENVIRONMENT. *Physiol* vol. 90 (1988).
6. Juárez, M. A. et al. Better late than never? Interannual and seasonal variability in breeding chronology of gentoo penguins at stranger point, Antarctica. *Polar Research* vol. 32 Preprint at <https://doi.org/10.3402/polar.v32i0.18448> (2013).
7. Bromwich, D. H. et al. Central West Antarctica among the most rapidly warming regions on Earth. *Nat Geosci* 6, 139–145 (2013).

QUESTION 3

a) Upload to GitHub

b) Share your repo with a partner and try to run their data pipeline. partner’s GitHub link:

- c) Reflect on running their code (300-500 words)
- d) Reflect on your own code based on your experience with your partner's code and their review of yours (300-500 words)