Wind support analysis

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2023-09-22

Wind support is an important energy resource for birds (1-4). Wind has been linked to the speed and routes of migrating white storks (*Ciconia ciconia*) (5,6). Thus, we investigated wind support as a predictor of route selection. We did not find it to be a significant predictor, and found neither a signature of selection nor of change over time. We excluded wind support from our final models, but present it here because wind is often considered to be important.

The first step is to determine which wind estimates to use. All of the wind estimates in these weather models are highly correlated. In addition, the height above ellipsoid values sent by the tags are error prone, especially when the tag is cold, and do not necessarily reflect the true height of the bird. For these two reasons, we felt it was sufficient to use only the wind estimate at the pressure level around the approximate average flight height of a migrating stork.

```
# libraries:
library(terra)
library(glmmTMB)
library(tidyverse)
# functions:
wind_support <- function(u,v,heading) {</pre>
  angle <- atan2(u,v) - heading/180*pi</pre>
  return(cos(angle) * sqrt(u*u+v*v))
cross_wind <- function(u,v,heading) {</pre>
  angle <- atan2(u,v) - heading/180*pi</pre>
  return(sin(angle) * sqrt(u*u+v*v))
wind speed <- function(u,v) {
  return(sqrt(u*u+v*v))
## Determine which level of wind to use by looking at the overall flight heights
# of white storks
# the annotated data file with the uplift and conspecific density values
a_data <- readRDS("/home/hbronnvik/Documents/storkSSFs/annotations/HR_030923.rds")
# all of the full, raw data downloaded from Movebank
files <- list.files("/home/hbronnvik/Documents/storkSSFs/full_data", pattern = ".rds", full.names = T)
# the geoid heights from EGM2008 https://www.agisoft.com/downloads/geoids/
egm <- terra::rast("/home/hbronnvik/Documents/storkSSFs/us_nga_egm2008_1.tif")</pre>
# take the geoid height (AKA geoid undulation) out of the
```

```
# height above ellipsoid to get height above geoid (AKA msl)
# start with a simple collection of all the heights above ellipsoid
# there can be a lot of error in these readings, so we remove the very large or very
# small values (although error exists in the plausible ones as well)
heights <- lapply(files, function(file){
  data <- readRDS(file)</pre>
  data <- data %>%
   # take out the bursts
   mutate(td = as.numeric(difftime(timestamp, lag(timestamp), units = "secs"))) %>%
   filter(td >= 300) %>%
   mutate(seq15 = round_date(timestamp, unit = "15 minutes")) %>%
    group by(seq15) %>%
   slice(1) %>%
   ungroup() %>%
   dplyr::select(-seq15, -td) %>%
   mutate(distance = geosphere::distVincentyEllipsoid(cbind(location.long, location.lat), cbind(lag(lo
           timediff = as.numeric(difftime(timestamp, lag(timestamp), units = "secs")),
           ground_speed_15 = distance/timediff) %>%
    # use only locations that are plausible and in-flight
    filter(ground_speed_15 < 50 & ground_speed_15 > 2)
  hae <- data %>%
   filter(height.above.ellipsoid > -100 & height.above.ellipsoid < 10000) %>%
   dplyr::select(timestamp, location.long, location.lat, height.above.ellipsoid)
})
heights <- data.table::rbindlist(heights)</pre>
# next, extract the geoid undulations at each of the locations that has HAE
heights$geoid_height <- terra::extract(egm, vect(heights,
                                                  geom = c("location.long",
                                                           "location.lat")))[ ,2]
# add on the height above mean sea level
heights$ha_msl <- heights$height.above.ellipsoid - heights$geoid_height
# find the average flight height above mean sea level,
# but try to use only the trustworthy ones by not allowing the birds to fly above the boundary layer
heights <- heights %>%
  filter(ha_msl < max(na.omit(a_data$blh)))</pre>
mean(heights$ha_msl)
## [1] 683.2945
# compare this mean to the mean heights of each pressure level in the annotations
log_heights <- lapply(15:28, function(x){</pre>
 level_h <- a_data[, x]</pre>
 level <- colnames(a_data)[x]</pre>
  info <- data.frame(level = level, mean = mean(na.omit(log(level_h))), sd = sd(na.omit(log(level_h))))
}) %>% reduce(rbind) %>% arrange(as.numeric(level))
# look at the heights of the levels
colfunc <- colorRampPalette(c("#0081A7", "#0098b0", "#00AFB9", "#7fc4b8", "#FED9B7", "#f7a58f", "#f27e7
pd <- a_data[, c(15:28)]
```

```
pd <- pd %>%
  pivot_longer(names_to = "level", values_to = "geoH", cols = names(pd)) %>%
  mutate(level = as.numeric(level),
          # the levels are skewed simply because low pressure exists at higher altitudes
          # we log normalize to take the mean
          log_geoH = log(geoH)) %>%
  arrange(level)
ggplot(pd, aes(log geoH, color = as.factor(level), fill = as.factor(level))) +
    geom histogram(bins = 1000) +
    labs(x = "Geopotential height", y = "Count") +
    scale_color_manual("Pressure level (mb)", values = colfunc(14)) +
    scale_fill_manual("Pressure level (mb)", values = colfunc(14)) +
    theme classic() +
    facet_wrap(~factor(level, levels = c("1000", "975", "950", "925", "900", "875", "850", "825", "800"
             1000
                                                                  925
                               975
                                                 950
                     20000
                                                                            Pressure level (mb)
   40000
                     10000
   20000
                                                                                 600
         -4-20246
                           4.85.25.66.0
                                              6.06.26.46.6
                                                               6.46.5.6.76.8
                                                                                 650
                                                                                 700
              900
                               875
                                                 850
                                                                  825
                                                                                 750
                                                                                 775
                                                                                 800
                                                             7.303540455055
          6.76.86.97.0
                             7.0 7.1 7.2
                                               7.2 7.3 7.4
Count
                                                                                 825
              800
                               775
                                                 750
                                                                  700
                                                                                 850
                                       20000
                                       15000
10000
5000
                                                         15000
                                                                                 875
                                                          5000
                                                                                 900
        7.4550556065
                          7.60.65.70.75.80
                                              7.73.80.83.90
                                                               7.98.08.08.10
                                                                                 925
             650
                               600
                                                                                 950
    20000
                     20000
                                                                                 975
    15000
                     15000
    10000
                      10000
                                                                                  1000
     5000
                      5000
                            8.308.358.40
           8.158.28.25
                               Geopotential height
```

Look at the mean log heights of the pressure levels log heights

```
level
##
                mean
## 1
        600 8.382277 0.02060264
## 2
        650 8.224674 0.02117622
## 3
        700 8.049903 0.02191177
## 4
        750 7.851134 0.02292309
## 5
        775 7.739583 0.02364638
## 6
        800 7.617418 0.02466032
## 7
        825 7.481895 0.02617267
```

```
## 8
        850 7.329089 0.02852916
## 9
        875 7.153118 0.03231931
## 10
        900 6.944613 0.03860282
        925 6.687230 0.04953549
## 11
## 12
        950 6.348549 0.07050391
## 13
        975 5.846427 0.12154267
## 14 1000 4.815541 0.37841110
## Finally, compare the flight heights to the pressure levels
mean(na.omit(log(heights$ha msl)))
## [1] 6.026083
sd(na.omit(log(heights$ha_msl)))
## [1] 1.328603
# read out files to annotate with the wind data from Movebank Env-DATA service at the given level
# https://www.movebank.org/cms/movebank-content/env-data
wind_file <- a_data %>%
  dplyr::select(timestamp, long, lat, individual.id) %>%
  mutate(timestamp = paste0(timestamp, ".000"),
         group = c(rep(c("a"), times = n()/4),
                   rep(c("b"), times = n()/4),
                   rep(c("c"), times = n()/4),
                   rep(c("d"), times = n()/4))) %>%
  rename("location-long" = long,
         "location-lat" = lat)
```

We found that the mean log height of the 950 mb pressure level for our data was 6.35 ± 0.07 sd and the mean log flight height of storks was approximately 6.02 ± 1.33 sd.

We calculated wind support using the north/south and east/west components of the wind (7) at 950 millibars of pressure.

```
## Explore the wind data to look for patterns
# after annotation, read in the files from Movebank Env-DATA
wind_files <- list.files("/home/hbronnvik/Documents/storkSSFs/ecmwf/winds", pattern = ".csv", full.name</pre>
# make the column names convenient
winds <- lapply(wind_files, read.csv) %>% reduce(rbind)
winds$X <- NULL
colnames(winds)
##
   [1] "timestamp"
##
   [2] "location.long"
  [3] "location.lat"
   [4] "individual.id"
##
##
   [5] "group"
  [6] "ECMWF.ERA5.PL.U.Wind"
##
  [7] "ECMWF.ERA5.PL.V.Wind"
   [8] "ECMWF.ERA5.SL.Wind..10.m.above.Ground.U.Component."
##
  [9] "ECMWF.ERA5.SL.Wind..100.m.above.Ground.U.Component."
## [10] "ECMWF.ERA5.SL.Wind..100.m.above.Ground.V.Component."
## [11] "ECMWF.ERA5.SL.Wind..10.m.above.Ground.V.Component."
```

```
colnames(winds)[2:3] <- c("long", "lat")</pre>
colnames(winds)[6:11] <- c("u_950", "v_950", "u_10m", "u_100m", "v_100m", "v_100m")
# turn the stamp back to an R format
winds <- winds %>%
  mutate(timestamp = as.POSIXct(timestamp, tz = "UTC"))
# also make the long/lat format match the a_data so that the join will recognize them
a data <- a data %>%
 mutate(long = as.character(long),
        lat = as.character(lat)) %>%
 mutate(long = as.numeric(long),
        lat = as.numeric(lat))
# add the wind data to the steps with their social density and w*
a_data <- full_join(a_data, winds) %>%
 mutate(cross_wind = cross_wind(u_950, v_950, heading),
         wind_support = wind_support(u_950, v_950, heading),
         wind_speed = wind_speed(u_950, v_950),
         wind_speed_100m = wind_speed(u_100m, v_100m),
         wind_speed_ground = wind_speed(u_10m, v_10m)) %>%
  rename(ud_pdf = UD_PDF,
         migrations = journey_number) %>%
  mutate(season = ifelse(grepl("fall", track), "post", "pre"))
# double-check our understanding that wind estimates from these weather
# models are highly correlated across pressure levels
check <- a data %>%
  dplyr::select(wind_speed_ground, wind_speed, wind_speed_100m) %>%
  # reduce the number of data points to make this faster
  group_by(wind_speed_ground) %>%
 slice(1) %>%
  ungroup() %>%
  rename("950 millibars" = wind_speed,
         "100 meters" = wind_speed_100m) %>%
  pivot_longer(cols = c("950 millibars", "100 meters"), names_to = "wind_level",
               values_to = "wind_speed")
ggplot(check, aes(wind_speed_ground, wind_speed)) +
  geom_point(alpha = .5) +
  geom_smooth(aes(group = wind_level, color = wind_level), method = "lm") +
  scale_color_manual(values = c("#0081A7", "#F07167")) +
  labs(x = "Wind speed at 10m above ground (m/s)",
       y = "Wind speed at pressure (m/s)",
       color = "Measurement \nheight") +
  theme_classic()
```

```
Wind speed at pressure (m/s)
                                                                             Measurement
                                                                             height
                                                                                  100 meters
                                                                                  950 millibars
                             5
                                                10
                                                                    15
                     Wind speed at 10m above ground (m/s)
# such strong correlation justifies the use of one pressure level rather than
# interpolating to an approximation of the bird's height
a_data %>%
  dplyr::select(c(wind_speed_ground, wind_speed, wind_speed_100m)) %>%
  corrr::correlate()
## # A tibble: 3 x 4
##
     term
                        wind_speed_ground wind_speed_100m
     <chr>>
                                                <dbl>
##
                                     <dbl>
                                                                 <dbl>
                                                0.900
## 1 wind_speed_ground
                                   NA
                                                                 0.978
                                                                 0.912
## 2 wind_speed
                                    0.900
                                               NA
                                    0.978
## 3 wind_speed_100m
                                                0.912
                                                                NA
# look at wind support distributions
# universal facet labels
fac_labs <- c("Fall", "Spring")</pre>
names(fac_labs) <- c("post", "pre")</pre>
support <- ggplot(a_data %>% group_by(wind_support) %>% slice(1) %>% ungroup(), aes(as.factor(migration
  geom_hline(yintercept = 0, lty = 2) +
  geom_boxplot() +
  theme classic() +
  labs(x = "Migrations", y = "Wind support (m/s)", fill = "Use case") +
  scale_color_manual(values = c("#0081A7", "#F07167")) +
  theme_classic() +
  theme(text = element_text(color = "black")) +
  facet_wrap(~season, labeller = labeller(season = fac_labs))
# look at wind speed distributions
```

```
speeds <- ggplot(a_data %>% group_by(wind_speed) %>% slice(1) %>% ungroup(), aes(as.factor(migrations),
  geom_boxplot() +
  theme_classic() +
  labs(x = "Migrations", y = "Wind speed (m/s)", fill = "Use case") +
  scale_color_manual(values = c("#0081A7", "#F07167")) +
  theme classic() +
  theme(text = element_text(color = "black")) +
  facet_wrap(~season, labeller = labeller(season = fac_labs))
cowplot::plot_grid(support, speeds, labels = c("A", "B"), ncol = 1,
           align = 'v', axis = 'l')
Α
                        Fall
                                                             Spring
Wind support (m/s)
                                                                                     Use case
                                                                                         FALSE
                                                                                         TRUE
    -20
                                         9
                                                   2
                                       Migrations
 В
                        Fall
                                                             Spring
  Wind speed (m/s)
                                                                                     Use case
                                                                                         FALSE
                                                                                         TRUE
                         5
                                         ġ
                                                               5
                                                                          8
                             6
                                     8
                                                   2
                                        Migrations
```

There is no sign in the distributions that we should expect selection (i.e. no difference between used and available) or to see a change over time (no shift in speeds given age). Still, we can check quantitatively by including wind support in our model.

```
# run the model once for each season
mods <- lapply(split(a_data, a_data$season), function(df){</pre>
 df <- df %>%
   mutate(stratum ID = as.factor(stratum),
          individual.id = as.numeric(individual.id))
 # build the formula
 TMB_struc <- glmmTMB(used ~ -1 + wind_support_z + sqrt_ud_z + w_star_z +</pre>
                        migrations_z + step_length_z + turning_angle_z +
                      (1|stratum ID) +
                      (0 + wind_support_z | individual.id) +
                      (0 + sqrt_ud_z | individual.id) +
                      (0 + w_star_z | individual.id) +
                      (0 + migrations_z | individual.id),
                    family = poisson,
                    data = df, doFit = FALSE,
                    map = list(theta = factor(c(NA, 1:4))),
                    start = list(theta = c(log(1e3), 0, 0, 0, 0)))
 TMB_M <- glmmTMB:::fitTMB(TMB_struc)</pre>
})
summary(mods[[1]]) # the fall
## Family: poisson (log)
## Formula:
## used ~ -1 + wind_support_z + sqrt_ud_z + w_star_z + migrations_z +
##
      step_length_z + turning_angle_z + (1 | stratum_ID) + (0 +
      wind support z | individual.id) + (0 + sqrt ud z | individual.id) +
##
      (0 + w_star_z | individual.id) + (0 + migrations_z | individual.id)
##
## Data: df
##
##
        AIC
                  BIC
                         logLik deviance df.resid
   444611.1 444738.4 -222295.6 444591.1
                                           2482870
##
## Random effects:
##
## Conditional model:
                                  Variance Std.Dev.
## Groups
                   Name
## stratum ID
                   (Intercept)
                                 1.000e+06 1.000e+03
## individual.id
                   wind_support_z 1.986e+00 1.409e+00
## individual.id.1 sqrt_ud_z
                                 5.612e+02 2.369e+01
## individual.id.2 w_star_z
                                 3.757e-01 6.129e-01
## individual.id.3 migrations_z 9.842e-05 9.921e-03
## Number of obs: 2482880, groups: stratum_ID, 24874; individual.id, 158
##
## Conditional model:
                    Estimate Std. Error z value Pr(>|z|)
## wind_support_z -0.172768 0.115080 -1.50
                                                  0.133
## sqrt_ud_z
                   12.841658
                             1.924152
                                          6.67 2.49e-11 ***
                   0.970650 0.065934
                                         14.72 < 2e-16 ***
## w_star_z
## migrations_z
                  -42.387177 0.591782 -71.63 < 2e-16 ***
## step_length_z
                    0.127719
                               0.008166
                                        15.64 < 2e-16 ***
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
```

```
summary(mods[[2]]) # the spring
##
   Family: poisson (log)
## Formula:
  used ~ -1 + wind_support_z + sqrt_ud_z + w_star_z + migrations_z +
##
       step_length_z + turning_angle_z + (1 | stratum_ID) + (0 +
##
       wind_support_z | individual.id) + (0 + sqrt_ud_z | individual.id) +
##
       (0 + w_star_z | individual.id) + (0 + migrations_z | individual.id)
##
  Data: df
##
##
         AIC
                   BIC
                          logLik deviance
                                             df.resid
    200398.9
              200518.3 -100189.4
                                  200378.9
                                              1135033
##
##
  Random effects:
##
##
##
  Conditional model:
   Groups
##
                    Name
                                    Variance
                                              Std.Dev.
##
   stratum_ID
                    (Intercept)
                                    1.000e+06 1000.0000
##
   individual.id
                    wind_support_z 2.351e+00
                                                 1.5332
##
   individual.id.1 sqrt_ud_z
                                    1.794e+01
                                                 4.2361
##
    individual.id.2 w_star_z
                                    8.783e-01
                                                 0.9372
    individual.id.3 migrations_z
                                    2.017e-04
                                                 0.0142
##
                                     stratum_ID, 11374; individual.id, 72
  Number of obs: 1135043, groups:
##
## Conditional model:
##
                    Estimate Std. Error z value Pr(>|z|)
## wind support z
                                 0.18806
                                           -0.97
                                                    0.334
                    -0.18158
## sqrt_ud_z
                     3.67355
                                 0.53651
                                            6.85 7.53e-12 ***
                     0.54272
                                 0.13390
                                            4.05 5.05e-05 ***
## w star z
## migrations_z
                   -41.15466
                                 0.78910
                                          -52.15
                                                  < 2e-16 ***
                     0.25766
                                 0.01094
                                           23.55
## step_length_z
                                                  < 2e-16 ***
## turning_angle_z -11.62879
                                 0.12299
                                          -94.55
                                                  < 2e-16 ***
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
```

As we could expect from the exploratory plots, we find no evidence of selection on wind support in either season.

References

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- Vansteelant W, Bouten W, Klaassen R, Koks B, Schlaich A, Van Diermen J, Van Loon E, Shamoun-Baranes J. 2015 Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales. Journal of Avian Biology 46, 25–39.
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