

Timing of moult for individual feathers

Birgit Erni^{a,b}

^aCentre for Statistics in Ecology, Environment and Conservation; ^bDepartment of Statistical Sciences, University of Cape Town, South Africa

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This vignette demonstrates the use of the `moult` package for individual primary feathers, using the `weaver` moult data.

`moult | primaries`

Introduction. The moult models (Underhill and Zucchini, 1988; Underhill *et al.*, 1990; Erni *et al.*, 2013) assume constant rate of feather mass accumulation throughout moult. This may not be a reasonable assumption. An alternative approach for evaluating the amount of feather mass accumulated over time, is to estimate start and duration separately for each feather, and then to add up the feather parts growing at a particular time (Remisiewicz *et al.*, 2009).

Here we will demonstrate how to estimate start and duration for each primary feather, using the weavers data in package `moult`. This vignette is partly intended to demonstrate how to use `moult` (Erni *et al.*, 2013) for individual feathers, and partly as a demonstration that one needs to be cautious regarding the results. Here we have used data type 3 and the parameter estimates are suspicious.

Weavers example.

```
library(moult)
head(weavers)
```

```
#          RDate Sex Year      Moult
# 1 1999-07-24  2 1999 55555555555
# 2 1999-07-24  1 1999 55555555555
# 3 2000-05-19  1 2000 55555555555
# 4 2002-10-21  1 2002 55555555555
# 5 2003-11-19  2 2003 55555555555
# 6 2004-12-03  4 2004 55555555555
```

We select only the first nine primary feathers, because the 10th is small, and not scored for all birds. Then we convert the complete moult score to a character vector, which is easier to split into individual feather scores. At the end we convert the individual moult scores to numeric values.

```
weavers$moult9 <- substr(weavers$Moult, 1, 9)
weavers$moult9 <- as.character(weavers$moult9)

l1 <- strsplit(weavers$moult9, "")
df <- data.frame(matrix(unlist(l1), ncol = 9, byrow=T))
df1 <- sapply(df, as.character)
head(df1)
```

```
#          X1 X2 X3 X4 X5 X6 X7 X8 X9
# [1,] "5" "5" "5" "5" "5" "5" "5" "5" "5"
# [2,] "5" "5" "5" "5" "5" "5" "5" "5" "5"
# [3,] "5" "5" "5" "5" "5" "5" "5" "5" "5"
# [4,] "5" "5" "5" "5" "5" "5" "5" "5" "5"
# [5,] "5" "5" "5" "5" "5" "5" "5" "5" "5"
# [6,] "5" "5" "5" "5" "5" "5" "5" "5" "5"
```

```
df2 <- apply(df, 2, FUN = as.numeric)
head(df2)
```

```
#          X1 X2 X3 X4 X5 X6 X7 X8 X9
# [1,] 5 5 5 5 5 5 5 5 5
# [2,] 5 5 5 5 5 5 5 5 5
# [3,] 5 5 5 5 5 5 5 5 5
# [4,] 5 5 5 5 5 5 5 5 5
# [5,] 5 5 5 5 5 5 5 5 5
```

```
# [6,] 5 5 5 5 5 5 5
```

Here we convert the individual moult score into a proportion of feather mass grown. We first write a function that will convert a score between 0 and 5 to PFMG (Remisiewicz *et al.*, 2009), then apply this function to every column (every primary feather).

```
f1 <- function(x) {
  ifelse(x == 0, 0,
         ifelse(x == 5, 1,
                ifelse(x >= 1 & x <= 4, x * 0.25 - 0.125, NA)))
}

df3 <- apply(df2, 2, FUN = f1)
weavers <- cbind(weavers, df3)
tail(weavers)
```

	RDate	Sex	Year	Moult	moult9	X1	X2	X3	X4	X5	X6	X7	X8
#	5277	2004-12-29	1	2004	5555555555	5555555555	1	1	1	1	1	1.000	1.000
#	5278	2004-12-29	1	2004	5555555555	5555555555	1	1	1	1	1	1.000	1.000
#	5279	2004-12-15	2	2004	5555555555	5555555555	1	1	1	1	1	1.000	1.000
#	5280	2004-09-03	2	2004	5555555555	5555555555	1	1	1	1	1	1.000	1.000
#	5281	2004-09-03	2	2004	5555555555	5555555555	1	1	1	1	1	1.000	1.000
#	5282	1995-04-08	0	1995	888555321	888555321	NA	NA	NA	1	1	0.625	0.375
#							X9						
#	5277						1.000						
#	5278						1.000						
#	5279						1.000						
#	5280						1.000						
#	5281						1.000						
#	5282						0.125						

```
weavers <- na.omit(weavers)
```

To calculate day of year or season we let 1 = 1 August. Days early in the year (before 1 August) are counted since the previous year's 1 August.

```
weavers$day <-
  ifelse(as.Date(weavers$RDate) < as.Date(paste(weavers$Year, "-08-01", sep = "")),
        as.Date(weavers$RDate) - as.Date(paste(weavers$Year - 1, "-07-31", sep = "")),
        as.Date(weavers$RDate) - as.Date(paste(weavers$Year, "-07-31", sep = "")))
```

```
weavers <- weavers[weavers$day > 50, ]

durationmean2ab <- function(duration, mean)
  { ab <- c(- mean / duration, 1 / duration)
    names(ab) <- c("intercept", "slope")
    return(ab)
  }
```

We will use data type 3 here, because there are 0's and 1's throughout the year, and it is hard to decide where set the cutoff. The default initial values do not seem to work very well here. Instead, for an initial estimate of mean start day, we took the average day where moult indeces were below 0.2, and for end day the mean day where moult indeces were above 0.8 (indicated by the red dots in the figures). An initial estimate for duration was obtained from the difference between these two. Standard deviation was estimated from the standard deviation in days with moult indeces below 0.2.

```
trajs <- matrix(NA, ncol = 2, nrow = 9)
par.est <- data.frame(duration = numeric(), start = numeric(), sd.start = numeric(),
                      se.dur = numeric(), se.start = numeric(), se.sd = numeric())

par(mfrow = c(3, 3), mar = c(4, 4, 2, 1))

for (prim in 1:9) {  # for primary 1 to 9
  ind <- 5 + prim
```

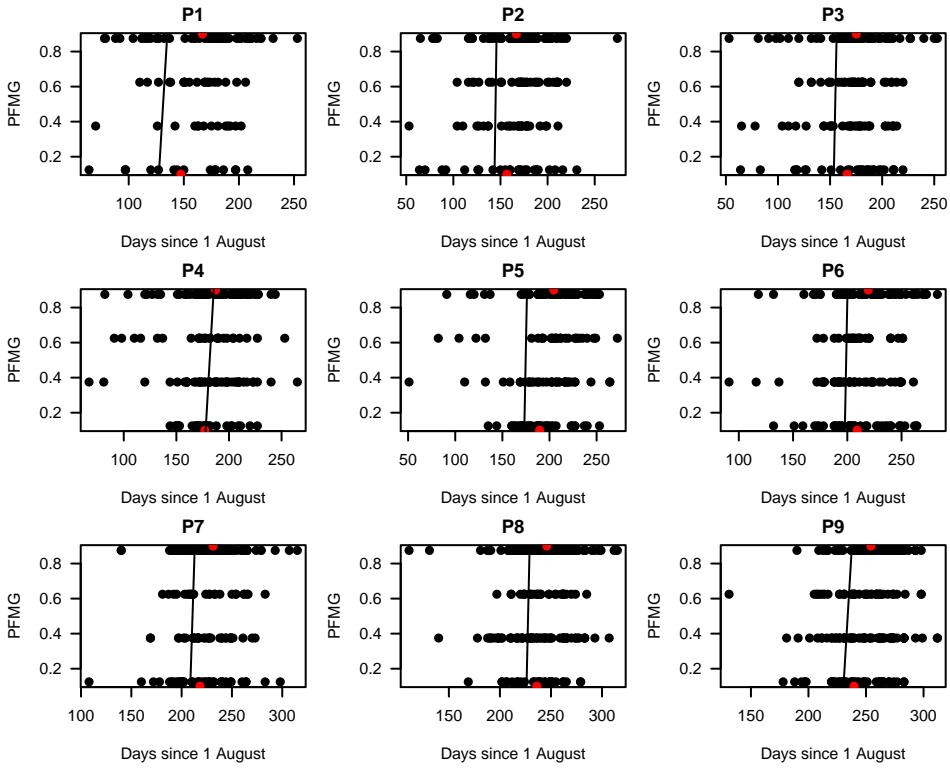


Fig. 1. Estimates of start and duration of moult for primaries 1 to 9 (line), with observed moult indeces (dots).

```

mi <- weavers[, c(ind, 15)]

names(mi) <- c("moult.index", "day")
head(mi)

start.init <- with(subset(mi, moult.index > 0 & moult.index < 0.2), mean(day))
dur.init <- with(subset(mi, moult.index > 0.8 & moult.index < 1), mean(day)) - start.init
sd.init <- with(subset(mi, moult.index > 0 & moult.index < 0.2), sd(day))

(inits <- c(dur.init, start.init, log(sd.init)))

plot(moult.index ~ day, data = subset(mi, moult.index > 0 & moult.index < 1), pch = 19,
     main = paste("P", prim, sep = ""), ylab = "PFMG", xlab = "Days since 1 August", las = 1)
points(start.init, 0.1, col = "red", pch = 19)
points(start.init + dur.init, 0.9, col = "red", pch = 19)

out <- moult(moult.index ~ day,
             data = subset(mi, moult.index > 0 & moult.index < 1),
             type = 3, prec = 0.125, start = inits)

df <- c(coef(out), sqrt(diag(out$vcov)))
par.est <- rbind(par.est, df)

traj <- durationmean2ab(coef(out), "duration"), coef(out, "mean"))

trajs[prim, ] <- traj

abline(traj, ylim = c(0, 1))

}

```

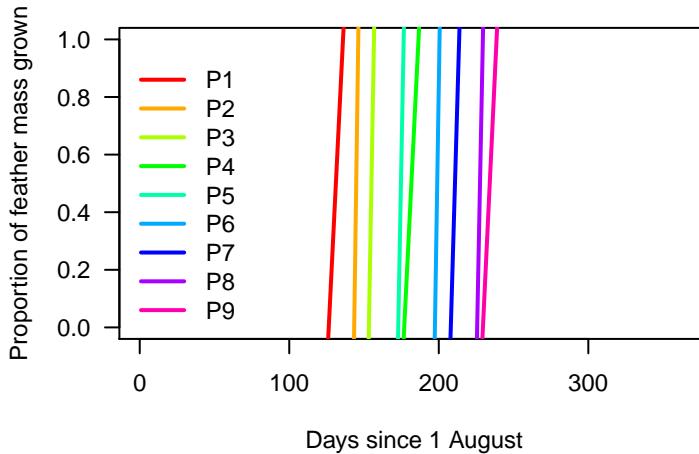


Fig. 2. Moult trajectories for individual primary feathers P1-P9, for the weavers data.

```
names(par.ests) <- c("duration", "start", "sd.start", "se.dur", "se.start", "se.sd")
```

For this document, warning messages were suppressed; there are many. Comparing the fitted moult trajectory lines in the above plots to the initial values (red dots), most durations seem too short. For primary 4, 5 and 8 some of the standard errors were not estimated, which is an indication that something went wrong during model fitting. Primary P4 has a huge standard deviation in start estimate, and fitting did not go much further than the initial values supplied.

Many of the lines are steeper and earlier than it seems they should be. I am not sure why this is, one possibility is the strong influence of outliers (individuals that have finished early). On the other hand, many birds are observed near completion, and few with moult scores < 0.2 , which suggests that the mean starting date was earlier than indicated by the red dot.

```
par.ests
```

	duration	start	sd.start	se.dur	se.start	se.sd
# 1	9.526721	126.4184	14.87146	1.28075431	1.735044516	0.006791316
# 2	2.722226	143.4177	16.09847	4.57021714	30.344034796	0.003991715
# 3	3.410115	153.2506	11.68898	0.14938186	0.124026253	0.003309588
# 4	9.550642	176.8884	38291.27415	NaN	NaN	NaN
# 5	3.631424	172.8880	12.54736	0.01345308	0.007865702	NaN
# 6	3.084635	197.4161	11.32102	0.04597952	0.045884812	0.042982458
# 7	5.582150	208.0421	12.58191	0.09995538	0.100044671	0.002753015
# 8	3.807188	225.6673	10.67192	NaN	NaN	NaN
# 9	9.111230	229.5354	20.31535	73.25520423	39.509822390	4.034548311

The following code will plot a trajectory for each primary.

```
plot(1:366, rep(0.5, times = 366), type = "n", ylim = c(0, 1), las = 1, lwd = 1,
     ylab = "Proportion of feather mass grown", xlab = "Days since 1 August")
for (i in 1:9) {
  abline(trajs[i, ], col = rainbow(9)[i], lwd = 2)
}
legend("bottomleft", col = rainbow(9), lty = 1, legend = paste("P", 1:9, sep = ""),
       bty = "n", lwd = 2)
```

Alternative Parameterization. Next, we repeat the above per-primary analysis using the alternative parameterization, which has the parameter *halfway date* instead of start of moult. This parameterization should be more robust to outliers and reduces the problem of strong negative correlation between the parameters duration and start of moult (Les Underhill, pers. comm., (Jackson, 2018)). The function implementing this parameterization, `moult_alternative`, is still in testing, and, as can be seen below, is not able to fit a model to many of the feathers, even though, based on simulations, generally it did seem more robust than with the original parameterization.

```
trajs <- matrix(NA, ncol = 2, nrow = 9)
par.ests <- data.frame(duration = numeric(), start = numeric(), sd.start = numeric(),
                       se.dur = numeric(), se.start = numeric(), se.sd = numeric())
```

```

par(mfrow = c(3, 3), mar = c(4, 4, 1, 1))

for (prim in 1:9) {    # for primary 1 to 9
  ind <- 5 + prim
  mi <- weavers[, c(ind, 15)]
  names(mi) <- c("moult.index", "day")
  head(mi)

  start.init <- with(subset(mi, moult.index > 0 & moult.index < 0.2), mean(day))
  dur.init <- with(subset(mi, moult.index > 0.8 & moult.index < 1), mean(day)) - start.init
  sd.init <- with(subset(mi, moult.index > 0 & moult.index < 0.2), sd(day))
  (inits <- c(dur.init, start.init + 0.5 * dur.init, log(sd.init)))

  plot(moult.index ~ day, data = subset(mi, moult.index > 0 & moult.index < 1), pch = 19,
       main = paste("P", prim, sep = ""), ylab = "PFMG", xlab = "Days since 1 August", las = 1)
  points(start.init, 0.1, col = "red", pch = 19)
  points(start.init + dur.init, 0.9, col = "red", pch = 19)
  points(start.init + 0.5 * dur.init, 0.5, col = "red", pch = 19)

  res <- try(out <- moult_alternative(moult.index ~ day, data = mi,
                                         type = 3, prec = 0.125, start = inits))
  ifinherits(res, "try-error")
  { ## if moult results in error, skip iteration
    df <- rep(NA, times = 6)
    par.est <- rbind(par.est, df)

    next
  }

## if no error continue with this
summary(out)

df <- c(coef(out), sqrt(diag(out$vcov)))
par.est <- rbind(par.est, df)

dur <- coef(out, "duration")
halfway <- coef(out, "mean")
start <- halfway - 0.5 * dur

traj <- durationmean2ab(dur, start)
trajs[prim, ] <- traj

abline(traj, ylim = c(0, 1))
}

```

```

names(par.est) <- c("duration", "halfway", "sd.halfway", "se.dur", "se.halfway", "se.sd")
par.est

```

#	duration	halfway	sd.halfway	se.dur	se.halfway	se.sd
# 1	13.072037	74.93997	23.00224	0.03253381	0.03251502	2.231065e-02
# 2	NA	NA	NA	NA	NA	NA
# 3	5.685129	129.55206	16.58625	NaN	NaN	NaN
# 4	9.667048	181.91603	38291.35112	237.27404154	207.32357946	2.405438e+02
# 5	3.903048	159.86771	13.47696	NaN	NaN	2.216015e-03
# 6	3.842941	185.24455	13.55142	0.11351239	0.10557067	7.748636e-02
# 7	6.901432	184.91856	16.11525	0.03380018	0.03385596	4.924107e-03
# 8	6.734519	193.22291	16.18455	0.04083220	0.04856659	2.753618e-02
# 9	14.029269	234.28628	25.16719	92.53574299	12.27085662	3.325179e+00

Here are the trajectories for primaries P1 to P9, estimated using the alternative moult parameterization.

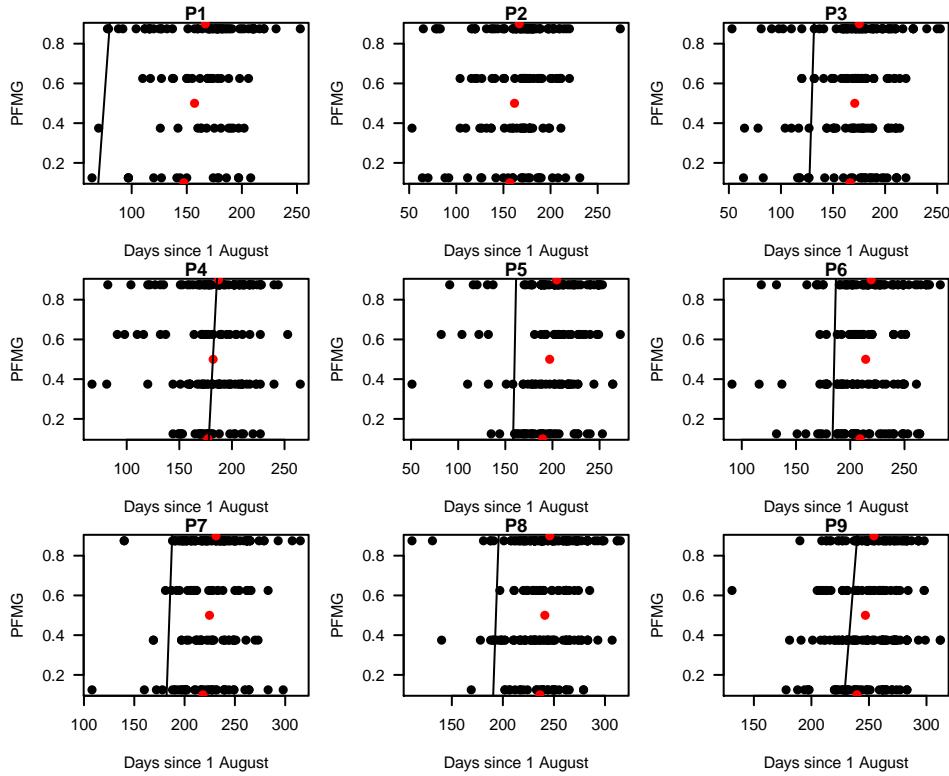


Fig. 3. Estimates of start and duration of moults for primaries 1 to 9 (line) using the alternative parameterization, with observed moult indeces (black dots) and initial estimates (red dots).

```
plot(1:366, rep(0.5, times = 366), type = "n", ylim = c(0, 1), las = 1, lwd = 1,
     ylab = "Proportion of feather mass grown", xlab = "Days since 1 August")
for (i in 1:9) {
  if (all(is.finite(trajs[i, ]))) abline(trajs[i, ], col = rainbow(9)[i], lwd = 2)
}
legend("bottomleft", col = rainbow(9), lty = 1, legend = paste("P", 1:9, sep = ""),
       bty = "n", lwd = 2)
```

The P2 trajectory could not be estimated; the P4 trajectory is on the initial values, and was therefore also not properly estimated.

Acknowledgments. This vignette was created using the [pimp](#) package.

References

- Erni B, Oschadleus HD, Bonnevie B, Altwegg R, Underhill LG (2013). “Moult: an R package to analyse moult in birds.” *Journal of Statistical Software*, **52**(8), 1–23. URL <https://www.jstatsoft.org/article/view/v052i08>.
- Jackson C (2018). *The moult and migration strategies of Lesser Sand Plover, Greater Sand Plover and Terek Sandpiper*. Ph.D. thesis, University of Cape Town, South Africa.
- Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB (2009). “Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa.” *Ardea*, **97**(3), 271–280. URL <http://www.bioone.org/doi/pdf/10.5253/078.097.0302>.
- Underhill LG, Zucchini W (1988). “A Model for Avian Primary Moult.” *Ibis*, **130**, 358–372.
- Underhill LG, Zucchini W, Summers RW (1990). “A Model for Avian Primary Moult Data Types Based on Migration Strategies and an Example Using the Redshank *Tringa totanus*.” *Ibis*, **132**, 118–123.

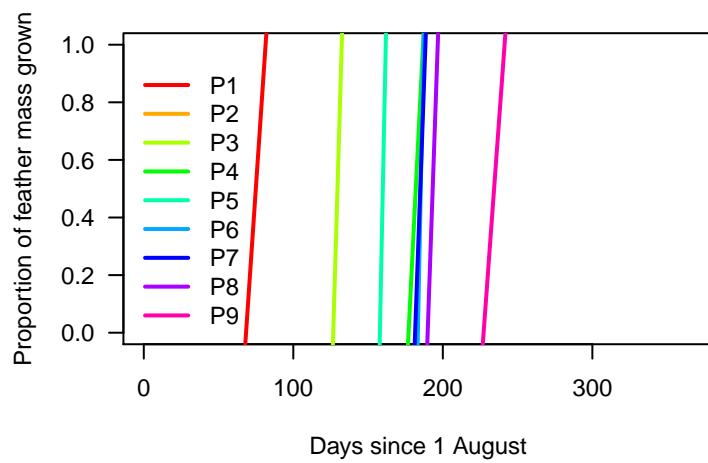


Fig. 4. Moulting trajectories for individual primary feathers P1-P9 using the alternative parameterization, for the weavers data.