

Reproducible analysis for: Individual flexibility in group foraging behaviour of reef manta rays (*Mobula alfredi*)

Raphaël Royauté

2024-02-21

Table of contents

0.1	Rationale	1
0.2	Packages and data import	1
0.3	Group vs. solo foraging	3
0.4	What explains variation in group leadership ?	3
0.5	Individual differences in group leadership compared between sexes, age and injury status	8
0.5.1	Male - female differences	8
0.5.1.1	Fit glmer models	8
0.5.1.2	Fit rptR models	12
0.5.1.3	Plot the model estimates	13
0.5.2	Juvenile - adult differences	16

0.1 Rationale

This is a reproducible script for all statistical models and their outputs presented in our article.

0.2 Packages and data import

Make sure to have these packages installed before running the code in this report

```
library(tidyverse); library(here); library(easystats);
library(kableExtra); library(lme4); library(effects)
library(marginaleffects); library(ggeffects); library(rptR)
library(gtsummary); library(ggthemes); library(patchwork)
library(tidybayes)
```

Import complete dataset

```
df = read.csv(here("data/data-clean/Manta Data_Annie.csv"),
              header=TRUE, sep=",", na.strings="NA", dec=".",
              strip.white=TRUE)
df %>%
  select(1:10) %>%
  head() %>%
  kable()
```

npid	id	day	year	nyear	site	clips	sex	size	maturity
P204	204	185	2016	year3	1	10	2	3	2
P204	204	185	2016	year3	1	10	2	3	2
P225	225	259	2016	year3	1	24	1	3	1
P281	281	259	2016	year3	1	24	2	3	2
P281	281	259	2016	year3	1	24	2	3	2
P302	302	259	2016	year3	1	24	1	3	1

Import group foraging dataset

```
df.group = read.csv(here("data/data-clean/group_rp.csv"),
                    header=TRUE, sep=",", na.strings="NA", dec=".",
                    strip.white=TRUE)
df.group$id = as.factor(df.group$id)
df.group$site = as.factor(df.group$site)
df.group$sex_f = as.factor(ifelse(df.group$sex=="1", "F", "M"))
df.group$size = as.factor(df.group$size)
df.group$maturity = as.factor(df.group$maturity)
df.group$plankton = as.factor(df.group$plankton)
df.group$shark_bite = as.factor(df.group$shark_bite)
df.group$anthropogenic = as.factor(df.group$anthropogenic)
df.group$Id = df.group$id

# Transform Time columns centered around 12:00pm expressed in hours
```

```

df.group$time_cen = hm(df.group$time)
df.group$time_cen = as.numeric(df.group$time_cen-hours(12))/3600

# subset with only individuals within groups
df.group = df.group[df.group$group==1,]
df.group=df.group[complete.cases(df.group$position),]
df.group %>%
  select(1:10) %>%
  head() %>%
  kable()

```

npid	id	obs_nb	rep_tot	day	year	nyear	site	clips	sex
P19	19	1	2	155	2016	year3	1	46	1
P19	19	2	2	155	2016	year3	1	46	1
P33	33	1	17	153	2016	year3	1	16	2
P33	33	2	17	155	2016	year3	1	46	2
P33	33	3	17	184	2016	year3	1	25	2
P33	33	4	17	184	2016	year3	1	25	2

0.3 Group vs. solo foraging

0.4 What explains variation in group leadership ?

We fit a binomial GLMM on leadership probability with the following covariates:

- Sex
- Age class
- Shark injury status
- Anthropogenic injury status
- Individual ID (random effect)

```

glmm.lead=glmer(leader ~
  sex_f + maturity +
  shark_bite + anthropogenic + (1|Id),
  family = "binomial",
  df.group)

summary(glmm.lead)

```

```

Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) [glmerMod]
Family: binomial ( logit )
Formula: leader ~ sex_f + maturity + shark_bite + anthropogenic + (1 | Id)
Data: df.group

```

AIC	BIC	logLik	deviance	df.resid
2152.9	2185.7	-1070.4	2140.9	1754

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.318	-0.650	-0.566	1.217	2.302

Random effects:

Groups	Name	Variance	Std.Dev.
Id	(Intercept)	0.2715	0.521

Number of obs: 1760, groups: Id, 322

Fixed effects:

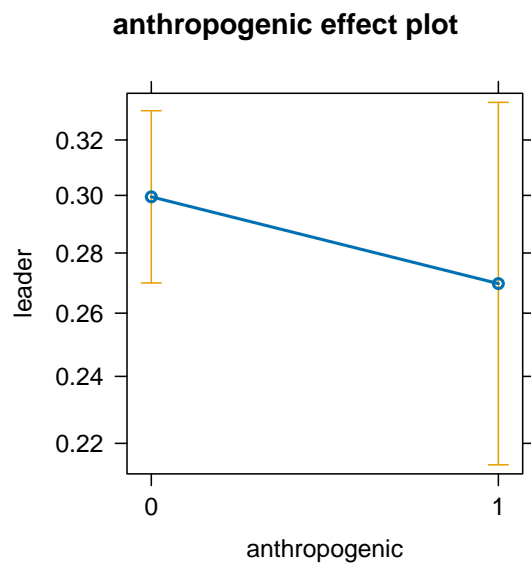
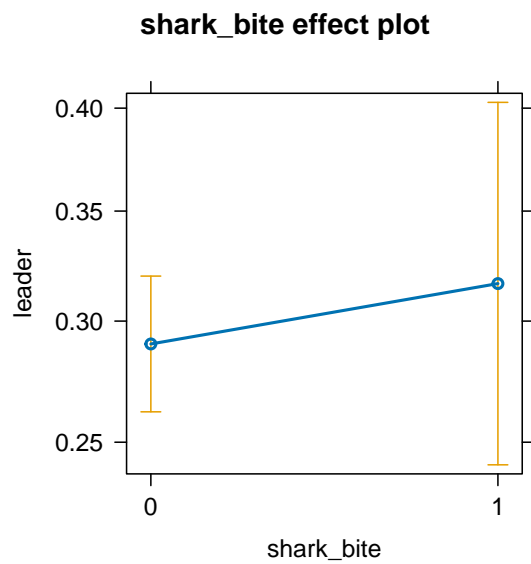
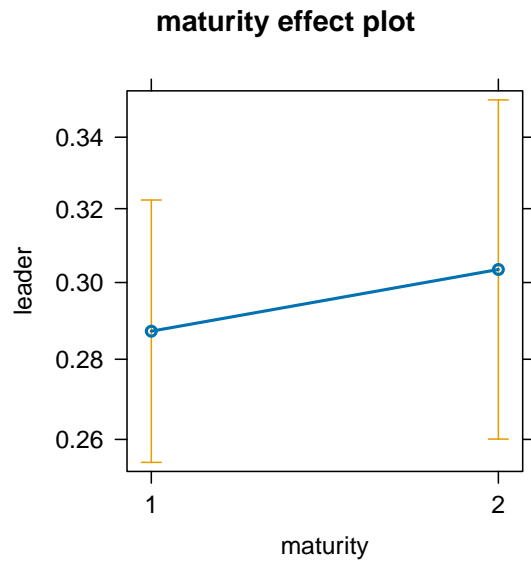
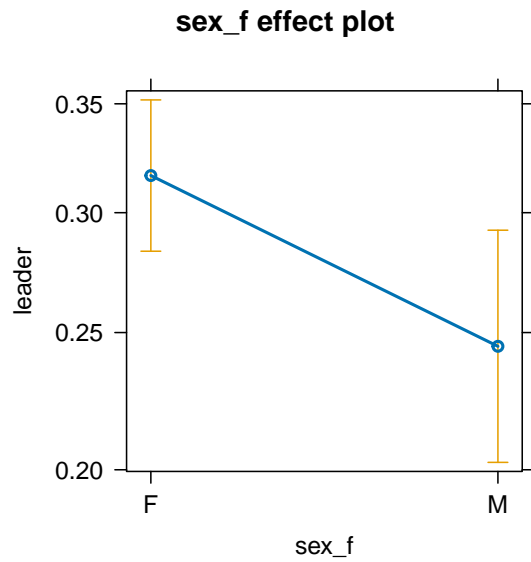
	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.78194	0.09655	-8.099	5.55e-16 ***
sex_fM	-0.35794	0.14851	-2.410	0.0159 *
maturity2	0.07813	0.13718	0.570	0.5690
shark_bite1	0.12525	0.20364	0.615	0.5385
anthropogenic1	-0.14638	0.17133	-0.854	0.3929

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	sex_fM	mtrty2	shrk_1
sex_fM		-0.310		
maturity2	-0.377	-0.282		
shark_bite1	-0.302	-0.024	0.051	
anthropgnc1	-0.305	0.007	-0.078	0.102

```
plot(allEffects(glmm.lead))
```



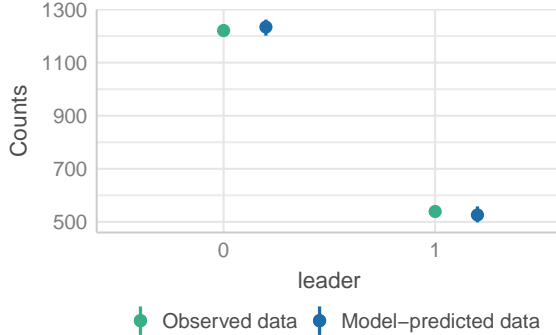
```
# Save model file
saveRDS(glmm.lead, file = here("outputs/mods/glmm.lead.rds"))
```

Inspect the model

```
check_model(glmm.lead)
```

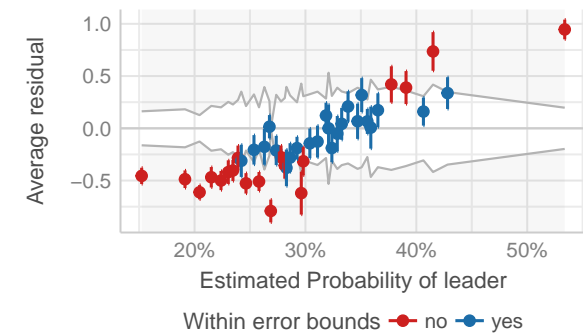
Posterior Predictive Check

Model-predicted intervals should include observed data point: Points should be within error bounds



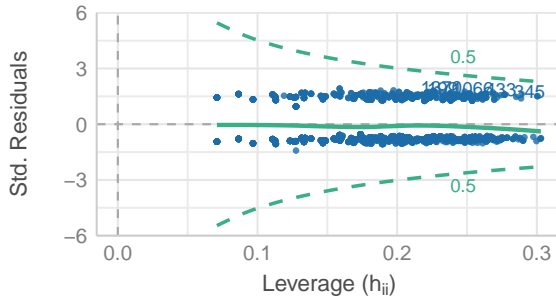
Binned Residuals

Points should be within error bounds



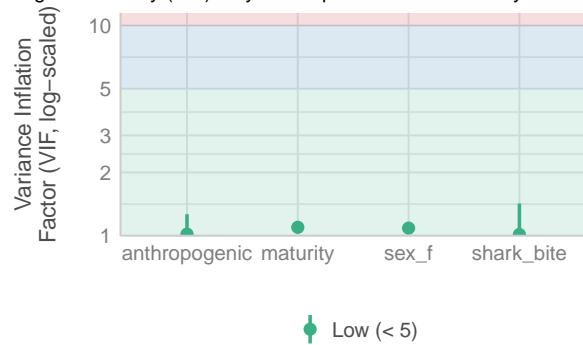
Influential Observations

Points should be inside the contour lines



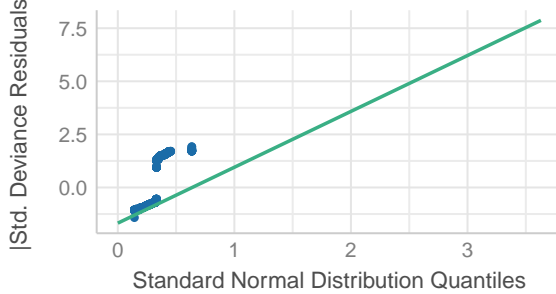
Collinearity

High collinearity (VIF) may inflate parameter uncertainty



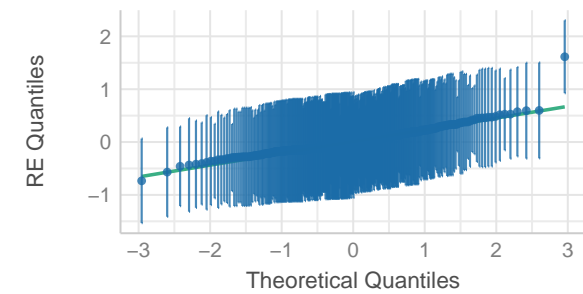
Normality of Residuals

Dots should fall along the line



Normality of Random Effects (Id)

Dots should be plotted along the line



Check R2 and repeatability

```
r2.lead = r2_nakagawa(glmm.lead, ci = T)
icc.lead = icc(glmm.lead, ci = T)
r2.lead; icc.lead

# Save files to avoid reloading
saveRDS(r2.lead, file = here("outputs/mods/r2.lead.rds"))
saveRDS(icc.lead, file = here("outputs/mods/icc.lead.rds"))
```

Get model summary in table format

```
tbl.glmm.lead = glmm.lead %>%
  tbl_regression(
    intercept = T,
    exponentiate = TRUE,
    pvalue_fun = ~ style_pvalue(.x, digits = 2)) %>%
  add_global_p() %>%
  bold_p(t = .05) %>%
  bold_labels() %>%
  italicize_levels() %>%
  add_nevent(location = "level")
tbl.glmm.lead
```

Characteristic	Event N	OR	95% CI	p-value
(Intercept)	539	0.46	0.38, 0.55	<0.001
sex_f				0.016
<i>F</i>	395	—	—	
<i>M</i>	144	0.70	0.52, 0.94	
maturity				0.57
<i>1</i>	344	—	—	
<i>2</i>	195	1.08	0.83, 1.41	
shark_bite				0.54
<i>0</i>	473	—	—	
<i>1</i>	66	1.13	0.76, 1.69	
anthropogenic				0.39
<i>0</i>	435	—	—	
<i>1</i>	104	0.86	0.62, 1.21	

We can now export the table in both word and html format

```
tbl.glmm.lead %>%
  as_gt() %>%
  gt::gtsave(filename = here("outputs/tables/tbl.glmm.lead.html"))

tbl.glmm.lead %>%
  as_gt() %>%
  gt::gtsave(filename = here("outputs/tables/tbl.glmm.lead.docx"))
```

0.5 Individual differences in group leadership compared between sexes, age and injury status

0.5.1 Male - female differences

0.5.1.1 Fit glmer models

```
glmm.lead.f = glmer(leader ~
  maturity +
  shark_bite + anthropogenic + (1|id),
  family = "binomial",
  subset(df.group, sex_f == "F"))
glmm.lead.m = glmer(leader ~
  maturity +
  shark_bite + anthropogenic + (1|id),
  family = "binomial",
  subset(df.group, sex_f == "M"))
summary(glmm.lead.f); summary(glmm.lead.m)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) [glmerMod]
Family: binomial (logit)
Formula: leader ~ maturity + shark_bite + anthropogenic + (1 | id)
Data: subset(df.group, sex_f == "F")
```

AIC	BIC	logLik	deviance	df.resid
1538.9	1564.4	-764.5	1528.9	1210

Scaled residuals:

Min	1Q	Median	3Q	Max
-0.8534	-0.6976	-0.6550	1.3714	1.5921

Random effects:

Groups	Name	Variance	Std.Dev.
id	(Intercept)	0.05108	0.226

Number of obs: 1215, groups: id, 205

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.81548	0.08899	-9.164	<2e-16 ***
maturity2	0.15263	0.14658	1.041	0.298

shark_bite1	0.28231	0.20398	1.384	0.166
anthropogenic1	0.01023	0.16630	0.062	0.951

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	mtrty2	shrkr_1
maturity2		-0.448	
shark_bite1		-0.345	0.030
anthropgnc1		-0.378	-0.010 0.088

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]

Family: binomial (logit)

Formula: leader ~ maturity + shark_bite + anthropogenic + (1 | id)

Data: subset(df.group, sex_f == "M")

AIC	BIC	logLik	deviance	df.resid
609.3	630.8	-299.7	599.3	540

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.7946	-0.5537	-0.4665	0.5572	2.7748

Random effects:

Groups Name	Variance	Std.Dev.
id (Intercept)	0.6399	0.8

Number of obs: 545, groups: id, 119

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.001829	0.001641	-610.64	<2e-16 ***
maturity2	-0.069563	0.001640	-42.41	<2e-16 ***
shark_bite1	-0.476913	0.001640	-290.88	<2e-16 ***
anthropogenic1	-0.482348	0.001640	-294.18	<2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

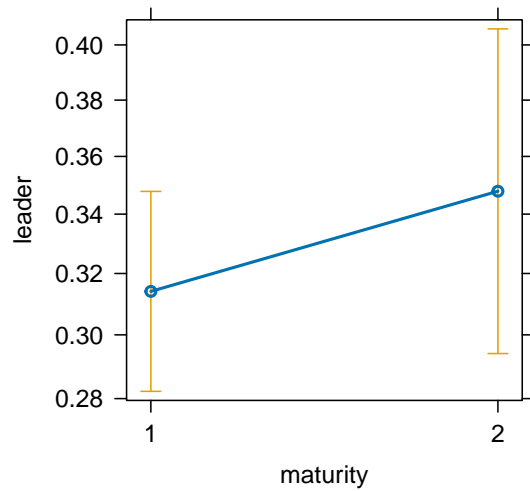
Correlation of Fixed Effects:

	(Intr)	mtrty2	shrkr_1
maturity2		0.000	
shark_bite1		0.000	0.000

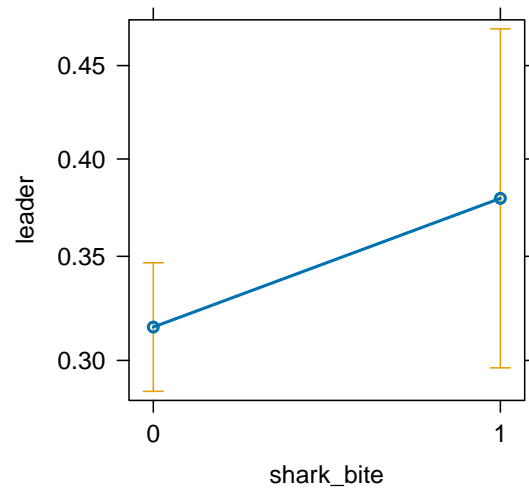
```
anthropgnc1 0.000 0.000 0.000  
optimizer (Nelder_Mead) convergence code: 0 (OK)  
Model failed to converge with max|grad| = 0.0430752 (tol = 0.002, component 1)
```

```
plot(allEffects(glm.lead.f)); plot(allEffects(glm.lead.f))
```

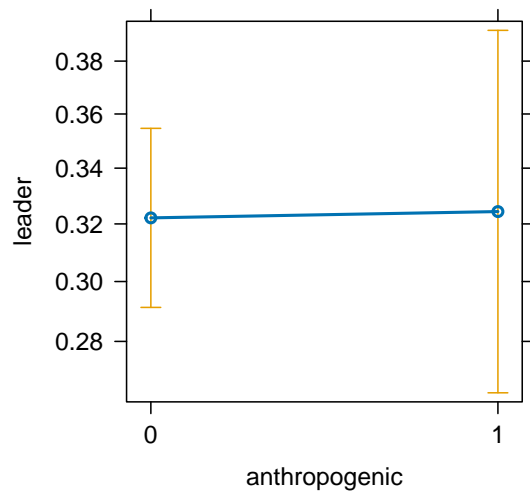
maturity effect plot

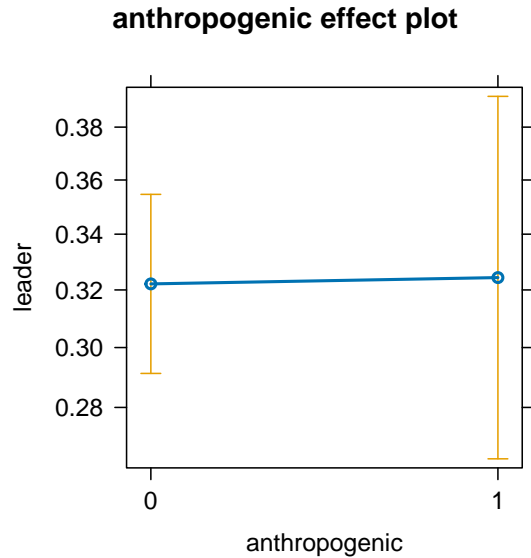
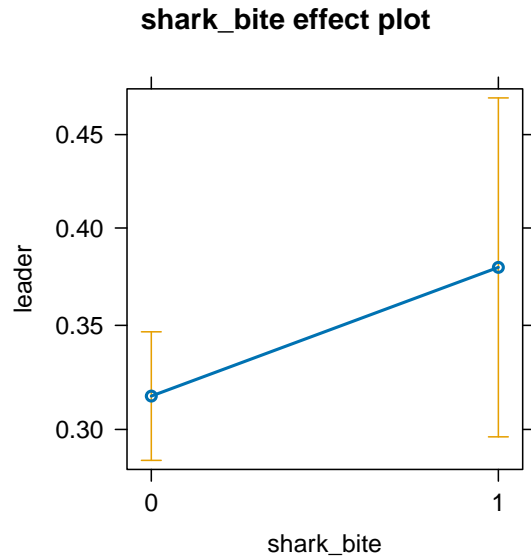
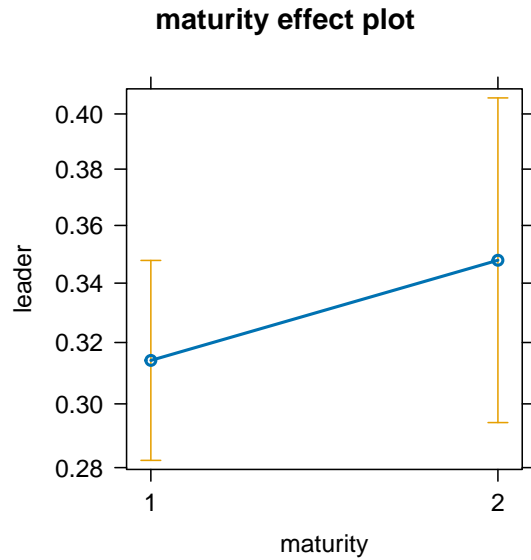


shark_bite effect plot



anthropogenic effect plot





```
# Save model file
saveRDS(glm.lead.f, file = here("outputs/mods/glm.lead.f.rds"))
saveRDS(glm.lead.m, file = here("outputs/mods/glm.lead.m.rds"))
```

The model does not converge properly with the male dataset. This comes from the fact that there are few adult males in the population. Because our question is now related to variance component, we keep the fixed effect structure the same regardless for consistency.

0.5.1.2 Fit rptR models

Adjusted repeatability

```
rpt.R.f = rpt(leader ~ maturity +
              shark_bite + anthropogenic + (1|id),
              grname = "id",
              datatype = "Binary",
              data = subset(df.group, sex_f == "F"))
rpt.R.m = rpt(leader ~ maturity +
              shark_bite + anthropogenic + (1|id),
              grname = "id",
              datatype = "Binary",
              data = subset(df.group, sex_f == "M"))

saveRDS(rpt.R.f, here("outputs/mods/rpt.R.f.rds"))
saveRDS(rpt.R.m, here("outputs/mods/rpt.R.m.rds"))
```

All variance components

```
rpt.V.f = rpt(leader ~ maturity +
              shark_bite + anthropogenic + (1|id),
              grname = c("id", "Fixed", "Residual"),
              datatype = c("Binary"),
              data = subset(df.group, sex_f == "F"),
              ratio = FALSE)
rpt.V.m = rpt(leader ~ maturity +
              shark_bite + anthropogenic + (1|id),
              grname = c("id", "Fixed", "Residual"),
              datatype = "Binary",
              data = subset(df.group, sex_f == "M"),
              ratio = FALSE)

saveRDS(rpt.V.f, here("outputs/mods/rpt.V.f.rds"))
saveRDS(rpt.V.m, here("outputs/mods/rpt.V.m.rds"))
```

All variance ratios

```
rpt.r2.f = rpt(leader ~ maturity +
               shark_bite + anthropogenic + (1|id),
               grname = c("id", "Fixed", "Residual"),
               datatype = c("Binary"),
               data = subset(df.group, sex_f == "F"),
```

```

        ratio = T)
rpt.r2.m = rpt(leader ~ maturity +
               shark_bite + anthropogenic + (1|id),
               grname = c("id", "Fixed", "Residual"),
               datatype = "Binary",
               data = subset(df.group, sex_f == "M"),
               ratio = T)
saveRDS(rpt.r2.f, here("outputs/mods/rpt.r2.f.rds"))
saveRDS(rpt.r2.m, here("outputs/mods/rpt.r2.m.rds"))

```

0.5.1.3 Plot the model estimates

Store all variance components

```

Vi_f = rpt.V.f$R_boot_link$id
Vi_m = rpt.V.m$R_boot_link$id
Vfe_f = rpt.V.f$R_boot_link$Fixed
Vfe_m = rpt.V.m$R_boot_link$Fixed
VR_f = rpt.V.f$R_boot_link$Residual
VR_m = rpt.V.m$R_boot_link$Residual
R_f = rpt.R.f$R_boot_link$id
R_m = rpt.R.m$R_boot_link$id

```

Put into formatted table

```

# Variance ratio difference figure
r2_Vi_f = rpt.r2.f$R_boot_link$id
r2_Vi_m = rpt.r2.m$R_boot_link$id
r2_Vfe_f = rpt.r2.f$R_boot_link$Fixed
r2_Vfe_m = rpt.r2.m$R_boot_link$Fixed
r2_VR_f = rpt.r2.f$R_boot_link$Residual
r2_VR_m = rpt.r2.m$R_boot_link$Residual

df = data.frame(r2_Vi = c(r2_Vi_f, r2_Vi_m),
                r2_Vfe = c(r2_Vfe_f, r2_Vfe_m),
                r2_VR = c(r2_VR_f, r2_VR_m),
                Sex = c(rep("F", length(r2_Vi_f)),
                       rep("M", length(r2_Vi_m)))) %>%
  pivot_longer(cols = r2_Vi:r2_VR,
               names_to = "v.compo",
               values_to = "var")

```

```
# Store effect sizes
df.2 = data.frame(delta_r2_Vi = r2_Vi_f - r2_Vi_m,
                  delta_r2_Vfe = r2_Vfe_f - r2_Vfe_m,
                  delta_r2_VR = r2_VR_f - r2_VR_m)
```

Plot

```
p1 = df %>%
  group_by(v.compo, Sex) %>%
  summarise(var = mean(var)) %>%
  ggplot(aes(y = var, x = Sex, fill = v.compo)) +
  geom_bar(position = "fill",
           stat = "identity", width = .2) +
  scale_fill_wsj(labels = c(
    bquote(V[fe]),
    bquote(V[i]),
    bquote(V[R])))) +
  ylab("Variance explained") +
  theme_bw(18) +
  labs(fill = "") +
  theme(legend.position = c(.9, .5))

delta.vi.r = df.2 %>%
  ggplot(aes(x = delta_r2_Vi * 100)) +
  stat_halfeye(alpha = .6) +
  geom_vline(xintercept = 0,
            linetype = "dashed") +
  xlab(bquote(Delta[V[i]])) +
  ylab("Density") +
  theme_bw(18) +
  ggtitle("Difference in variance explained (%)")

delta.vfe.r = df.2 %>%
  ggplot(aes(x = delta_r2_Vfe * 100)) +
  stat_halfeye(alpha = .6) +
  geom_vline(xintercept = 0,
            linetype = "dashed") +
  xlab(bquote(Delta[V[fe]])) +
  ylab("Density") +
  theme_bw(18)
```

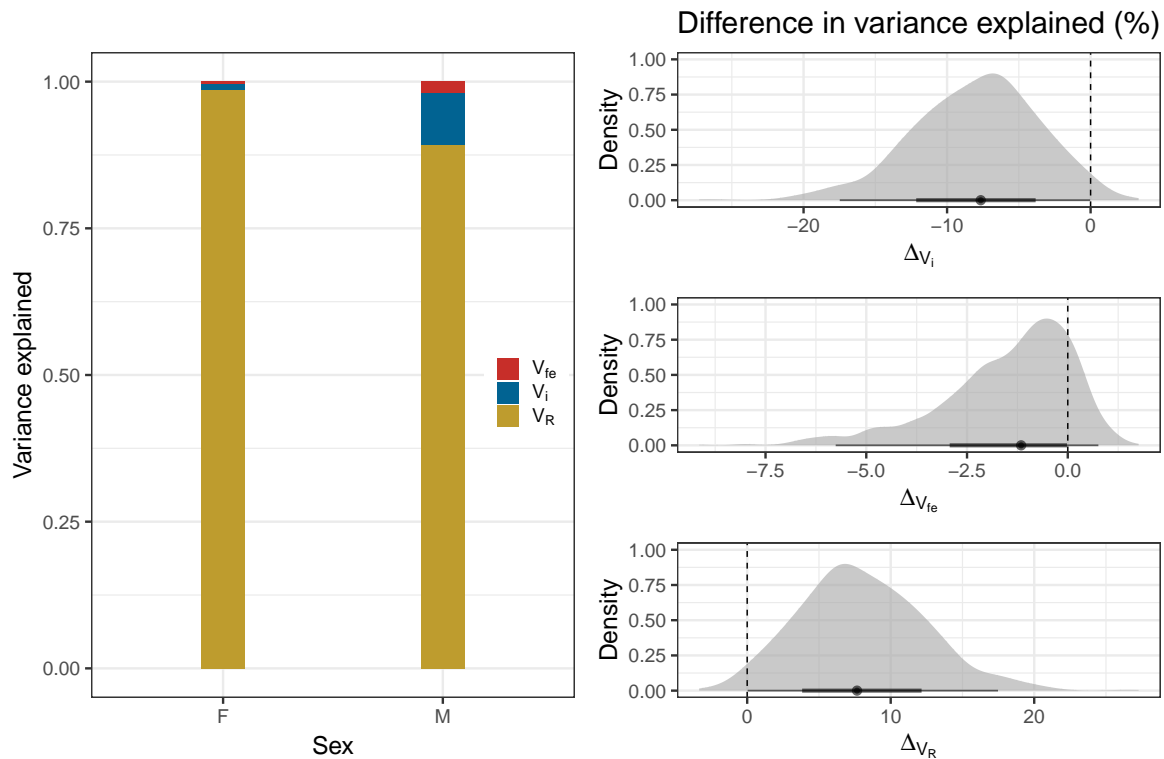
```

delta.vr.r = df.2 %>%
  ggplot(aes(x = delta_r2_VR * 100)) +
  stat_halfeye(alpha = .6) +
  geom_vline(xintercept = 0,
             linetype = "dashed") +
  xlab(bquote(Delta[V[R]])) +
  ylab("Density") +
  theme_bw(18)

delta.v.r = delta.vi.r / delta.vfe.r / delta.vr.r

delta.v.r = p1 + (delta.vi.r / delta.vfe.r / delta.vr.r)
delta.v.r

```



```

ggsave(filename = "outputs/figs/delta.v.r.jpeg", delta.v.r,
        width = 12, height = 8)
ggsave(filename = "outputs/figs/delta.v.r.pdf", delta.v.r,
        width = 12, height = 8)

```

0.5.2 Juvenile - adult differences

0.5.3