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

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Table of contents

Rationale	1
Packages and data import	2
What explains group vs. solo foraging? (TODO)	3
Null	3
What explains group size? (TODO)	4
Null	4
Model fitting	4
AIC model comparison	4
What explains variation in group leadership?	4
Model fitting and checks	4
Plots and tables	9
Individual differences in group leadership compared between sexes, age and injury	
status	13
Male - female differences	13
Juvenile - adult differences	18
Injured - non-injured differences	23
Are these differences statistically significant?	27

Rationale

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

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

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
P413	413	174	2016	year3	1	5	2	3	2
P423	423	185	2016	year3	1	10	1	4	2
P423	423	185	2016	year3	1	10	1	4	2
P423	423	185	2016	year3	1	10	1	4	2

Import group foraging dataset

```
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 aroun 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[1:10,] %>%
    select(1:10) %>%
    kable(digits = 2)
```

npid	id	obs nb	rep_tot	dav	year	nyear	site	clips	sex
	10						1	10	
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
P33	33	5	17	184	2016	year3	1	25	2
P33	33	6	17	184	2016	year3	1	25	2
P33	33	7	17	214	2016	year3	1	8	2
P33	33	8	17	215	2016	year3	1	1	2

What explains group vs. solo foraging? (TODO)

TODO ### Models tested

Null

Abiotic Site, current, time to high tide Biotic (external) Plankton, number of mantas (scaled) Abiotic + Biotic (ext) Site, current, time to high tide, plankton, number of mantas (scaled)

What explains group size? (TODO)

TODO ### Models tested

Null

Abiotic Site, current, time to high tide Biotic (external) Plankton, number of mantas (scaled) Abiotic + Biotic (ext) Site, current, time to high tide, plankton, number of mantas (scaled for control)

Model fitting

```
# glmm.group.size.null = glmer(group_size ~ 1 + (1|id),
# family=poisson,
# df)
#
# glmm.group.size.abio = glmer(group_size ~ 1 + (1|id),
# family=poisson,
# df)
```

AIC model comparison

What explains variation in group leadership?

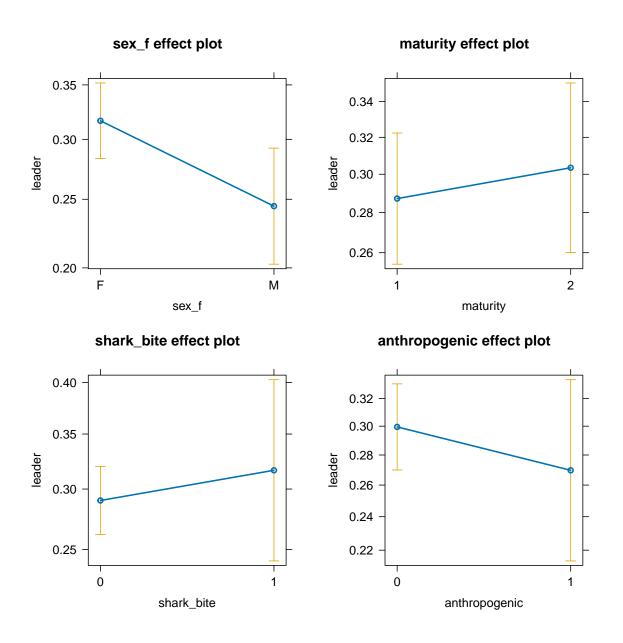
Model fitting and checks

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)

```
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
          2185.7 -1070.4
 2152.9
                           2140.9
                                     1754
Scaled residuals:
          1Q Median
  Min
                       3Q
                             Max
-1.318 -0.650 -0.566 1.217 2.302
Random effects:
Groups Name
                   Variance Std.Dev.
                          0.521
       (Intercept) 0.2715
Number of obs: 1760, groups: Id, 322
Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)
              sex_fM
                         0.14851 - 2.410
              -0.35794
                                          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
```

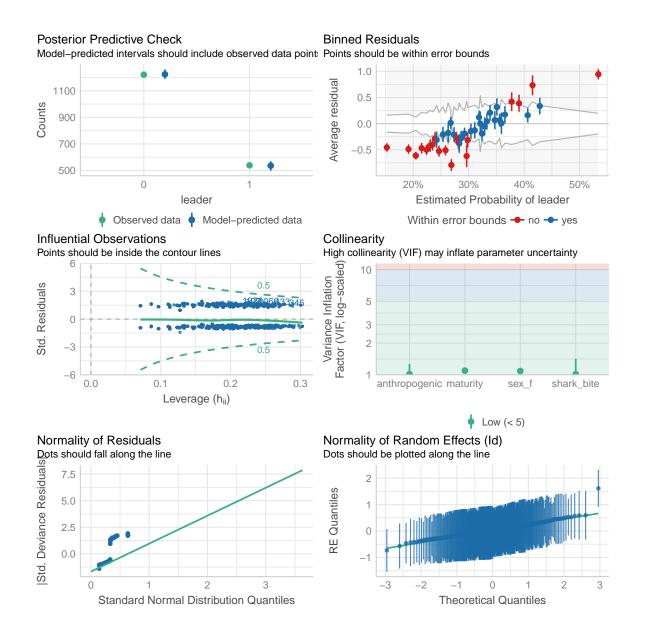
plot(allEffects(glmm.lead))



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

Inspect the model

check_model(glmm.lead)



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
F	395			
M	144	0.70	0.52, 0.94	
maturity				0.57
1	344			
2	195	1.08	0.83, 1.41	
shark_bite				0.54
0	473			
1	66	1.13	0.76, 1.69	
anthropogenic			,	0.39
0	435			
1	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"))
```

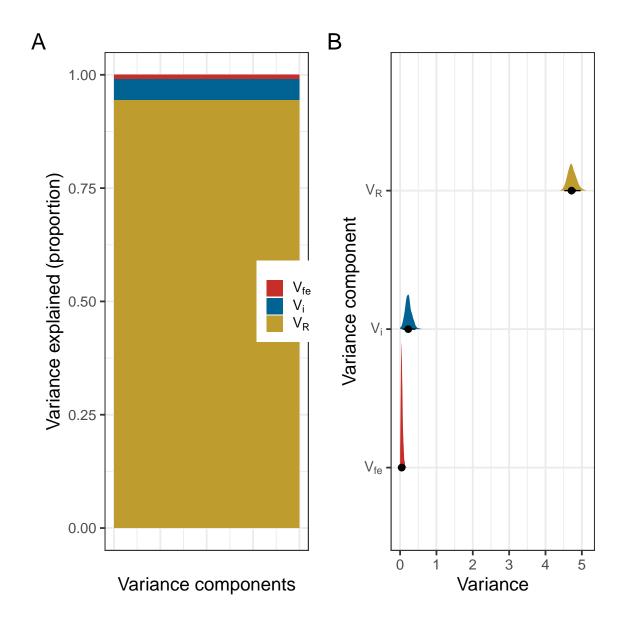
Plots and tables

We can get a full breakdown of the % of variance explained by all components in the model (fixed and random effects) using the rpt() function in the rptR package.

```
rpt.V.lead = rpt(leader ~ sex_f + maturity + shark_bite +
                      anthropogenic + (1|id),
               grname = c("id", "Fixed", "Residual"),
               datatype = c("Binary"),
              parallel = T,
               data = df.group,
               ratio = F)
saveRDS(rpt.V.lead, file = here("outputs/mods/rpt.V.lead.rds"))
rpt.r2.lead = rpt(leader ~ sex_f + maturity + shark_bite +
                      anthropogenic + (1|id),
              grname = c("id", "Fixed", "Residual"),
              datatype = c("Binary"),
              parallel = T,
               data = df.group,
               ratio = T)
saveRDS(rpt.r2.lead, file = here("outputs/mods/rpt.r2.lead.rds"))
```

Next we can combine all this information in figure format

```
p1 = df.compo.r2 \%
  group_by(v.compo) %>%
  summarise(var = mean(var)) %>%
  ggplot(aes(y = var * 100, x = 0, fill = v.compo)) +
  geom_bar(position = "fil1",
           stat = "identity", width = .02) +
  scale_fill_wsj(labels = c(
    bquote(V[fe]),
    bquote(V[i]),
    bquote(V[R]))) +
  xlab("Variance components") +
  ylab("Variance explained (proportion)") +
  theme_bw(18) +
  theme(legend.position = c(.9, .5),
        legend.title = element_blank(),
        axis.text.x = element_blank(),
        axis.ticks.x = element_blank())
p2 = df.compo.V \%>\%
  ggplot(aes(y = v.compo, x = var, fill = v.compo)) +
  stat_halfeye() +
  scale_fill_wsj() +
  scale_y_discrete(labels = c(
    bquote(V[fe]),
    bquote(V[i]),
    bquote(V[R]))) +
  xlab("Variance") +
  ylab("Variance component") +
  theme_bw(18) +
  theme(legend.position = "none")
var.compo = p1 + p2 +plot_annotation(tag_levels = 'A')
var.compo
```



Finally we can export these values in table form

	Variance_component	Median	CI_low	CI_high	\overline{pd}
2	Vi	0.22	0.07	0.42	1
1	Vfe	0.04	0.01	0.11	1
3	VR	4.72	4.52	4.97	1

	Variance_explained	Median	CI_low	CI_high	pd
2	r2_Vi	4.63	1.58	7.89	1
1	$r2_Vfe$	0.87	0.21	2.26	1
3	r2_VR	95.37	92.11	98.42	1

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

We can further investigate whether the magnitude of individual differences varies among meaningful biological categories such as sex, age or injury status. To do so, we fit one model for each subset of the data and compute the distribution of the different variance component through bootstrapping. We can then test whether among-, within-individual or fixed effect variance differs between the different subset by computing the difference between the distribution of each subset considered: ΔV . The overlap of the 95 % confidence interval of this distribution with 0 indicates whether the differences are statistically significant. The scale on which to make the comparison can be either on the latent scale with the logit link in a binomial glmm or on the original data scale. Here we estimated variances on the latent scale but calculated the difference in terms of % difference from a reference level (sex: females, maturity: juveniles, injury: not injured).

Male - female differences

Given that females are more frequently seen leading the group, it seems plausible that females are more consistent in their leadership preferences. As a result, we would expect less among-individual differences in leadership if females are highly biased toward leading the group.

Fit glmer models

The model does not converges properly with the male dataset. This comes from that 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.

Fit rptR models

Adjusted repeatability

All variance components

```
rpt.V.f = rpt(leader ~ maturity + shark_bite +
                      anthropogenic + (1|id),
              grname = c("id", "Fixed", "Residual"),
              datatype = c("Binary"),
              parallel = T,
              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",
              parallel = T,
              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"),
              parallel = T,
               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",
              parallel = T,
               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"))
```

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
```

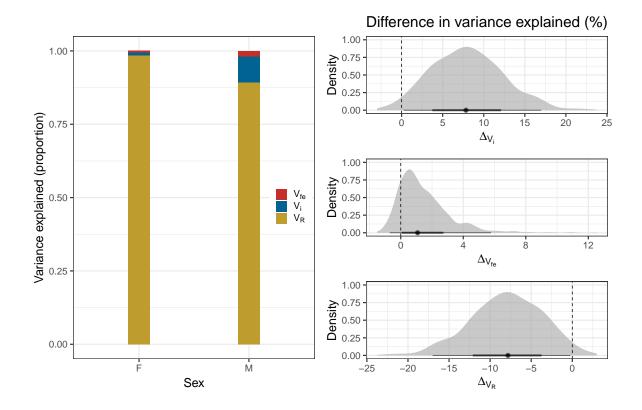
Put into formated table

```
# Variance ratio difference figure (deltaV = Vmales - Vfemales)
r2_Vi_f = rpt.r2.f$R_boot_link$id
r2_Vi_m = rpt.r2.m$R_boot_link$fixed
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.sex = data.frame(r2_Vi = c(r2_Vi_f, r2_Vi_m),
```

Plot

```
p1 = df.sex %>%
  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 (proportion)") +
  theme_bw(18) +
  labs(fill = "") +
  theme(legend.position = c(.9, .5))
delta.vi.r = df.sex.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.sex.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.sex.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
```



Juvenile - adult differences

We hypothesized that adult individuals have more experience and are therefore more likely to lead the foraging group. Similarly to females, we expect less among-individual variation in this class compared to juveniles.

Fit glmer models

```
subset(df.group, maturity == "2"))

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

Fit rptR models

Adjusted repeatability

All variance components

All variance ratios

Plot the model estimates

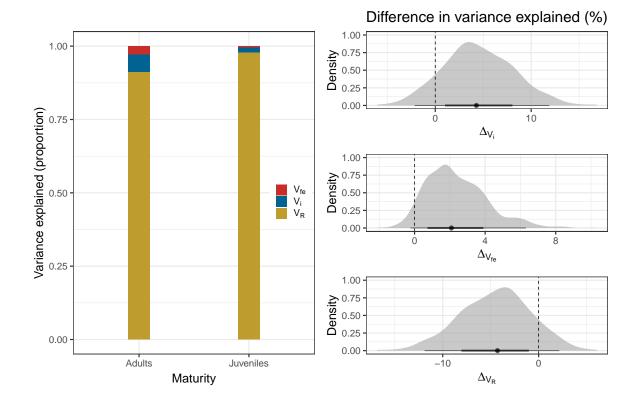
Store all variance components

```
Vi_j = rpt.V.j$R_boot_link$id
Vi_a = rpt.V.a$R_boot_link$id
Vfe_j = rpt.V.j$R_boot_link$Fixed
Vfe_a = rpt.V.a$R_boot_link$Fixed
VR_j = rpt.V.j$R_boot_link$Residual
VR_a = rpt.V.a$R_boot_link$Residual
R_j = rpt.R.j$R_boot_link$id
R_a = rpt.R.a$R_boot_link$id
```

Put into formated table

Plot

```
p1 = df.mat %>%
  group_by(v.compo, Maturity) %>%
  summarise(var = mean(var)) %>%
  ggplot(aes(y = var, x = Maturity, 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 (proportion)") +
  theme_bw(18) +
  labs(fill = "") +
  theme(legend.position = c(.9, .5))
delta.vi.r = df.mat.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.mat.2 %>%
  ggplot(aes(x = delta_r2_Vfe * 100)) +
  stat_halfeye(alpha = .6) +
  geom_vline(xintercept = 0,
```



Injured - non-injured differences

Here we're considering combining both anthropogenic and shark bite injury with the hypothesis that injured individuals have less chance of being at the front of the group and therefore should be more consistent in their positioning in the group.

Fit glmer models

Fit rptR models

Adjusted repeatability

```
saveRDS(rpt.R.ni, here("outputs/mods/rpt.R.ni.rds"))
saveRDS(rpt.R.i, here("outputs/mods/rpt.R.i.rds"))
```

All variance components

All variance ratios

Plot the model estimates

Store all variance components

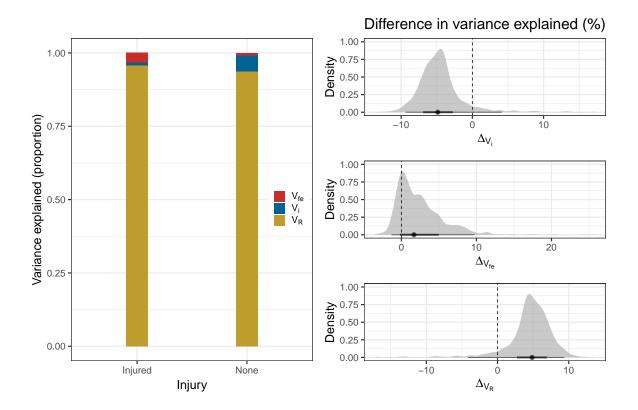
```
Vi_ni = rpt.V.ni$R_boot_link$id
Vi_i = rpt.V.i$R_boot_link$id
Vfe_ni = rpt.V.ni$R_boot_link$Fixed
Vfe_i = rpt.V.i$R_boot_link$Fixed
VR_ni = rpt.V.ni$R_boot_link$Residual
VR_i = rpt.V.i$R_boot_link$Residual
R_ni = rpt.R.ni$R_boot_link$id
R_i = rpt.R.i$R_boot_link$id
```

Put into formated table

```
r2_Vi_ni = rpt.r2.ni$R_boot_link$id
r2_Vi_i = rpt.r2.i$R_boot_link$id
r2 Vfe ni = rpt.r2.ni$R boot link$Fixed
r2 Vfe i = rpt.r2.i$R boot link$Fixed
r2_VR_ni = rpt.r2.ni$R_boot_link$Residual
r2_VR_i = rpt.r2.i$R_boot_link$Residual
df.inj = data.frame(r2_Vi = c(r2_Vi_ni, r2_Vi_i),
                r2_Vfe = c(r2_Vfe_ni, r2_Vfe_i),
                r2_{VR} = c(r2_{VR_ni}, r2_{VR_i}),
                Injury = c(rep("None", length(r2_Vi_ni)),
                        rep("Injured", length(r2_Vi_i)))) %>%
  pivot_longer(cols = r2_Vi:r2_VR,
               names_to = "v.compo",
               values_to = "var")
df.inj.2 = data.frame(delta r2 Vi = r2 Vi i - r2 Vi ni,
                   delta_r2_Vfe = r2_Vfe_i - r2_Vfe_ni,
                   delta_r2_VR = r2_VR_i - r2_VR_ni)
```

Plot

```
scale_fill_wsj(labels = c(
    bquote(V[fe]),
    bquote(V[i]),
    bquote(V[R]))) +
  ylab("Variance explained (proportion)") +
  theme bw(18) +
  labs(fill = "") +
  theme(legend.position = c(.9, .5))
delta.vi.r = df.inj.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.inj.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.inj.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
```



Are these differences statistically significant?

We can calculate the median and 95 % CI for the distribution of the difference between males and females. I'm using the describe_posterior() function from the bayestestR package here as it has nice option to summarize distributions. A positive value indicates that females are more variable for a given variance component expressed in % points relative to the total variance. The width of the 95 % CI indicates the precision of our estimates and the 'probability of direction' (pd) indicates the probability that the effect differs from 0. This metric is based on the proportion of values that are of the same sign as the median. pd values above 0.975 are roughly equivalent to a statistically-significant p-value with $\alpha=0.05$ for a two-sided test.

```
tbl_delta_r2_sex = describe_posterior(df.sex.2*100) %>%
  data.frame() %>%
```

```
mutate("Variance_component" = as.factor(Parameter)) %>%
 mutate(Variance_component = fct_recode(Variance_component,
            Delta_Vi = "delta_r2_Vi",
            Delta_Vfe = "delta_r2_Vfe",
            Delta_VR = "delta_r2_VR")) %>%
 select(c(11, 2, 4 :6)) %>%
 kable(digits = 2)
tbl_delta_r2_maturity = describe_posterior(df.mat.2*100) %>%
 data.frame() %>%
 mutate("Variance_component" = as.factor(Parameter)) %>%
 mutate(Variance_component = fct_recode(Variance_component,
            Delta_Vi = "delta_r2_Vi",
            Delta_Vfe = "delta_r2_Vfe",
            Delta_VR = "delta_r2_VR")) %>%
 select(c(11, 2, 4 :6)) %>%
 kable(digits = 2)
tbl_delta_r2_injury = describe_posterior(df.inj.2*100) %>%
 data.frame() %>%
 mutate("Variance_component" = as.factor(Parameter)) %>%
 mutate(Variance_component = fct_recode(Variance_component,
            Delta Vi = "delta r2 Vi",
            Delta_Vfe = "delta_r2_Vfe",
            Delta_VR = "delta_r2_VR")) %>%
 select(c(11, 2, 4 :6)) %>%
 kable(digits = 2)
tbl delta r2 sex; tbl delta r2 maturity; tbl delta r2 injury
```

	Variance_component	Median	CI_low	CI_high	pd
2	Delta_Vi	7.83	0.24	16.99	0.98
1	Delta_Vfe	1.08	-0.70	5.77	0.85
3	$Delta_VR$	-7.83	-16.99	-0.24	0.98

	Variance_component	Median	CI_low	CI_high	pd
2	Delta_Vi	4.29	-2.15	11.89	0.89
1	$Delta_Vfe$	2.09	-0.23	6.32	0.96
3	$Delta_VR$	-4.29	-11.89	2.15	0.89

	Variance_component	Median	CI_low	CI_high	\overline{pd}
2	Delta_Vi	-4.85	-9.38	4.14	0.93
1	$Delta_Vfe$	1.67	-1.32	9.77	0.78
3	$Delta_VR$	4.85	-4.14	9.38	0.93