SECTION A

A1

(a) A smallholder visits a market to purchase stock. After examining all of the stock available, she creates a shortlist of 4 Jacob sheep, 8 Hebridean sheep and 12 Cotswold sheep.

(i) How many ways could she select 10 sheep (ignoring breed) from her shortlist?

[~10% marks]

After further consideration, the smallholder decides to purchase 2 Jacob, 4 Hebridean and 4 Cotswold sheep from the shortlist.

(ii) How many ways could she have selected this combination from the shortlist of sheep?

[~15% marks]

(iii) On returning to the farm, the sheep are randomly placed in a row of individual holding pens. What is the probability that the sheep are lined up in breed groups? [Answers must be shown in factorial form as well as in decimal form.]

[~20% marks]

(b) A continuous random variable, X, has a cumulative distribution function, F, given by:

$$F(x) = \begin{cases} 0 \text{ for } x < 0 \\ \frac{x^4}{4}(x+3) \text{ for } 0 \le x \le 1 \\ 1 \text{ for } x > 1 \end{cases}$$

(i) Find $p(X \le 0.7 | X > 0.5$¿.

[~15% marks]

(ii) Find an expression for the probability density function $f(x)$.

[~10% marks]

(iii) Given $Y = \frac{3}{X} + 4$, find $Var(Y)$.

[~30% marks]

A1 sample answer

a(i): Answer: $24C_{10}$

```
nJacob = 4; nHeb = 8; nCostwold = 12;
totalSheep = nJacob+nHeb+nCostwold;
Q1aPart1 = nchoosek(totalSheep,10)
```

```
Q1aPart1 = 1961256
```

After further consideration, the small holder decides to purchase 2 Jacob, 4 Hebridean and 4 Cotswold sheep from the shortlist.

a(ii) Answer: $4C_2 \times 8C_4 \times 12C_4$

```
Q1aPart2=nchoosek(nJacob,2)*nchoosek(nHeb,4)*nchoosek(nCostwold,4)
```

```
Q1aPart2 = 207900
```

a(iii) Answer:

- Number of permutations of n items which consist of j distinct subgroups of size $k_1, \ldots, k_j = P = \dfrac{n!}{k_1!k_2!k_3!}$
- permutations: $P = \dfrac{10!}{2!4!4!}$
- number of ways to have lined by breed group = $3!$
- probability = number of ways lined by breed group/total number of permutations

```
PermAll = factorial(10)./(factorial(2)*factorial(4)*factorial(4))
```

```
PermAll = 3150
```

```
Q1aPart3ProbByBreed = factorial(3)/PermAll
```

```
Q1aPart3ProbByBreed = 0.0019
```

(b) (i) Answer:

- $p\left(X \le 0.7 \middle| X > 0.5\right) = \dfrac{p(0.5 < X \le 0.7)}{p(X > 0.5)}$

```
Fx = @(x) (x.^4).*(x+3)./4;
Q1bPart1 = (Fx(0.7)-Fx(0.5))./(1-Fx(0.5))
```

```
Q1bPart1 = 0.1771
```

b(ii) Answer*:*

- expand: $F(x) = \frac{x^5}{4} + \frac{3x^4}{4}$
- differentiate *cdf*: $f(x) = \frac{\mathrm{dF}}{\mathrm{dx}} = \frac{5x^4}{4} + \frac{12x^3}{4}$ if $0 \le x \le 1$ and 0 otherwise

b(iii) Given, $Y = \frac{3}{X} + 4$ find $\mathrm{Var}(Y)$

$$\mathrm{Var}(Y) = \mathrm{Var}\left(\frac{3}{X} + 4\right) = \mathrm{Var}\left(\frac{3}{X}\right) = 9\mathrm{Var}\left(\frac{1}{X}\right)$$

$$9\mathrm{Var}\left(\frac{1}{X}\right) = 9\left[E\left(\frac{1}{X^2}\right) - E\left(\frac{1}{X}\right)^2\right]$$

$$E\left(\frac{1}{X^2}\right) = \int_0^1 \frac{1}{x^2}\left(\frac{5x^4}{4} + \frac{12x^3}{4}\right)\mathrm{dx} = \frac{1}{4}\int_0^1 (5x^2 + 12x)\mathrm{dx} = \frac{1}{4}\left[\frac{5x^3}{3} + \frac{12x^2}{2}\right]_0^1 = \frac{23}{12}$$

$$E\left(\frac{1}{X}\right) = \int_0^1 \frac{1}{x}\left(\frac{5x^4}{4} + \frac{12x^3}{4}\right)\mathrm{dx} = \frac{1}{4}\int_0^1 (5x^3 + 12x^2)\mathrm{dx} = \frac{1}{4}\left[\frac{5x^4}{4} + \frac{12x^3}{3}\right]_0^1 = \frac{21}{16}$$

```
EX2 = 23/12;
EX = 21/16;
Q1bPart3 = 9*(EX2-EX^2)
```

```
Q1bPart3 = 1.7461
```

A2

An ecologist is modelling an endangered population of lizards that reproduces seasonally. Her model includes adults and juveniles as distinct categories, and represents the following life-cycle events in each season:

- A proportion p of adults survives to the next season.
- A proportion q of juveniles survives to the next season and become adults.
- Each adult produces, on average, r offspring that hatch as juveniles in the next season.

(a) If j_n is the number of juveniles in the nth season and a_n is the number of adults, show that this model can be represented as a linear system:

$$z_{n+1} = M z_n$$

where:

$$z_n = \begin{pmatrix} j_n \\ a_n \end{pmatrix} \quad \text{and} \quad M = \begin{pmatrix} 0 & r \\ q & p \end{pmatrix}$$

Note any additional assumptions you have made about the population in deriving this relationship.

[~25% marks]

(b) The ecologist estimates that p = 0.1, q = 0.5 and r = 2.2 are suitable parameter values for the lizards she is studying. Find the eigenvalues and eigenvectors of M given these values.

[~30% marks]

(c) In a given year, if there are 19 juveniles and 20 adults, what do you calculate, using this model, for the expected numbers of juveniles and adults 25 years later?

[~25% marks]

(d) What will be the ratio of juveniles to adults in the long term (as n goes to infinity), according to this model?

[~20% marks]

A2 sample answer

a) We have the following update equations:

$j_{n+1} = ra_n$,

$a_{n+1} = qj_n + pa_n$

expressing the survival and reproduction relationships in the model. This corresponds directly to the linear system given. It is necessary to assume that reproduction occurs before mortality.

b) The characteristic equation for M is

$0 = \det(M - \lambda I) = \lambda^2 - p\lambda - rq$

with solutions $\lambda = (p \pm \sqrt{(p^2 + 4rq)}) / 2$.

For $p = 0.1$, $q = 0.5$ and $r = 2.2$ we have $\lambda_1 = 1.1$ and $\lambda_2 = -1$.

Eigenvector for $\lambda_1 = 1.1$:

We have we have $(M - 1.2I)\mathbf{v}_1 = 0$, which reduces to

$-1.1x + 2.2y = 0$

$0.5x - y = 0$

and hence $v_1 = \alpha \begin{pmatrix} 2 \\ 1 \end{pmatrix}$

Eigenvector for $\lambda_2 = -1$:

We have we have $(M - I)\mathbf{v}_2 = 0$, which reduces to

$x + 2.2y = 0$

$0.5x + 1.1y = 0$

and hence $v_2 = \alpha \begin{pmatrix} -2.2 \\ 1 \end{pmatrix}$

c) Let $z_0 = \begin{pmatrix} 19 \\ 20 \end{pmatrix}$. Since $\lambda_1 \neq \lambda_2$ the eigenvectors of M form a basis, so we can express $\mathbf{z}_0$ in terms of them. We have $z_0 = \alpha_1 v_1 + \alpha_2 v_2$, i.e.

$$\begin{pmatrix} 19 \\ 20 \end{pmatrix} = \alpha_1 \begin{pmatrix} 2 \\ 1 \end{pmatrix} + \alpha_2 \begin{pmatrix} -2.2 \\ 1 \end{pmatrix}$$

which we solve to get $\alpha_1 = 15$ and $\alpha_2 = 5$.

Then we can write

$$z_n = \alpha_1 \lambda_1^n v_1 + \alpha_2 \lambda_2^n v_2 = 15(1.1)^n \begin{pmatrix} 2 \\ 1 \end{pmatrix} + 5(-1)^n \begin{pmatrix} -2.2 \\ 1 \end{pmatrix}$$

So for n = 25:

$$z_{25} = 15(1.1)^{25} \begin{pmatrix} 2 \\ 1 \end{pmatrix} + 5(-1)^{25} \begin{pmatrix} -2.2 \\ 1 \end{pmatrix} = 10.83 \begin{pmatrix} 30 \\ 15 \end{pmatrix} - \begin{pmatrix} -11 \\ 5 \end{pmatrix}$$

so j_{25} = 10.83*30 + 11 = 336.04 and a_{25} = 10.83*15 + 5 = 157.52.

d) The long-term behaviour is dominated by $\mathbf{v}_1$, i.e.

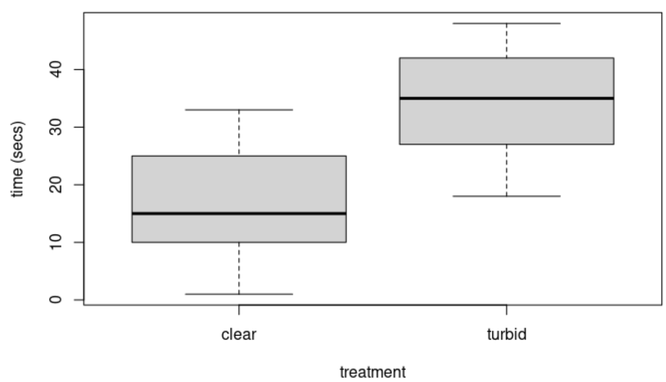
$$z_n \rightarrow \alpha_1 \lambda_1^n v_1 = 15(1.1)^n \begin{pmatrix} 2 \\ 1 \end{pmatrix}$$

so the ratio of juveniles to adults will tend towards 2:1.

SECTION B

B3

(a) A behavioural ecologist wants to study the impact of turbidity on risk taking by minnows. Individual fish were tested in an assay where they were placed in a refuge and the time taken to emerge into an open arena was recorded. Thirteen fish were tested in a tank with clear water, and ten fish in one with turbid water.



For the clear treatment, he obtains a mean, $\bar{x}_1$, of 17.62 s, and for the turbid treatment, $\bar{x}_2$, of 33.50 s. The respective Sums of Squares are SS_1 = 1331.08 and SS_2 = 964.50.

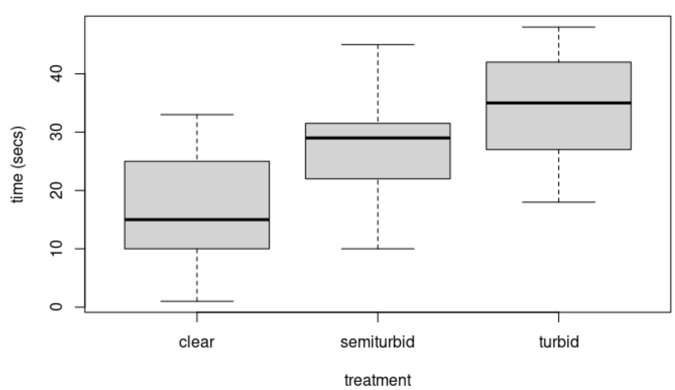
Test whether the turbidity affected the time to leave refuge (showing your work).

[~25% marks]

(b) Provide a sentence that you could use to report these results in a scientific paper.

[~10% marks]

(c) The behavioural ecologist now adds an additional treatment in which the water is semi-turbid, and tests 11 fish under such conditions. Combining the newly acquired data, he obtains:



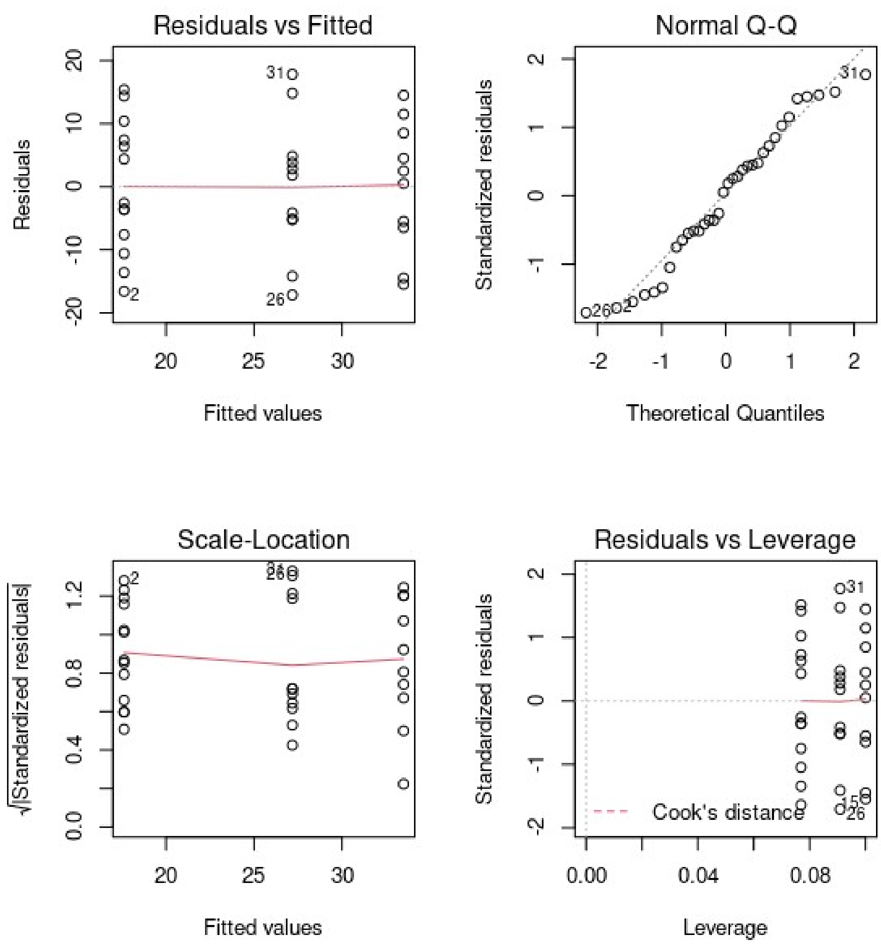
He uses a One-Way ANOVA to compare the different treatments:

	SS	Df	MS	F
Treatment	1478.8	**??**	**??**	**??**
Residuals	**??**	**??**	**??**	
Total	4928.0	33		

Complete the table (i.e. the cells with the symbol **??**). What conclusion would you draw about the effect of water turbidity on the time to leave refuge?

[~30% marks]

(d) What would you conclude from the diagnostic plots he obtained?



[~15% marks]

(e) Our behavioural ecologist also runs some Tukey's Honest Significant Differences tests:

```
Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = time ~ treatment, data = minnows)

$treatment
                       diff        lwr       upr
semiturbid-clear   9.566434  -1.069160  20.20203
turbid-clear      15.884615   4.964773  26.80446
turbid-semiturbid  6.318182  -5.025066  17.66143
```

Given the results above, write a sentence or two that you could use to summarise the omnibus test and the Tukey's tests in a scientific publication.

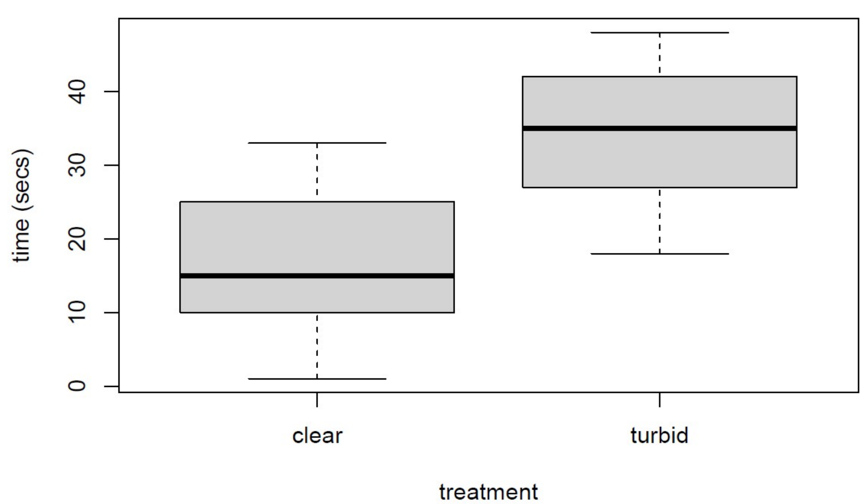
[~20% marks]

```
minnows<-read.csv("B3_data.csv",stringsAsFactors = TRUE)
```

```
minnows_2treat<-subset(minnows,treatment!="semiturbid")
minnows_2treat$treatment<-as.factor(as.character(minnows_2treat$treatment))
```

Make a plot

```
plot(time~treatment,data=minnows_2treat, ylab="time (secs)")
```



We need a t-test.

$\bar{x_1} - \bar{x_2}$= 17.62 - 33.50 = -15.88

s_p=sqrt((1331.08+964.5)/((13-1)+(10-1)))=10.456

$s_{\bar{x}_1-\bar{x}_2}$=10.456* sqrt(1/13+1/10)=4.398

t = -15.88 / 4.398 = -3.61

Our estimated t is larger than t_{crit} with 21 df, which is ~2.09 (for 20 df from the table). So, we can reject the null hypothesis and accept the alternative hypothesis that there is a difference between the two treatments.

Marking (5 points):1 for choosing the correct test, 0.5 each for difference of means, s_p, $s_{\bar{x}_1-\bar{x}_2}$, t, t_{crit} and the correct df (for a total of 3 marks), and 1 point for drawing the correct conclusion.

```
t.test(time ~ treatment, data = minnows_2treat, var.equal = TRUE)
```

```
##
##  Two Sample t-test
##
## data:  time by treatment
## t = -3.612, df = 21, p-value = 0.001636
## alternative hypothesis: true difference in means between group clear and group turbid is not equal t
## 95 percent confidence interval:
##  -25.030195  -6.739036
## sample estimates:
##  mean in group clear mean in group turbid
##             17.61538             33.50000
```

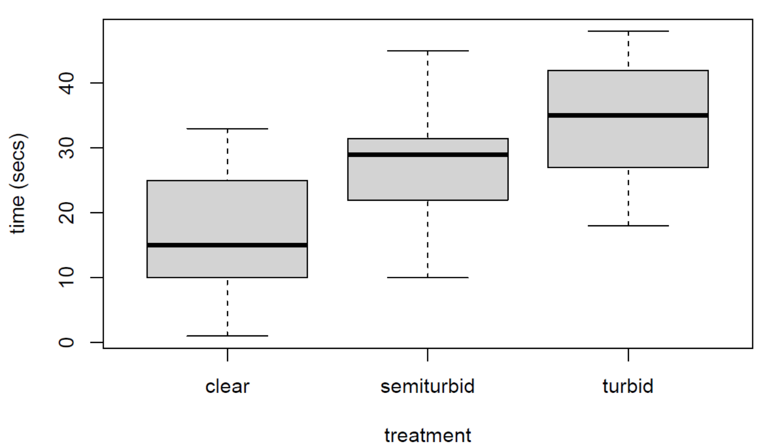
b) sentence for paper [10% marks 2 marks]

Minnows took longer to leave cover in turbid than in clear water (t_{21}=3.61,p<0.05).

[describing the direction of the effect, 1 mark; 0.5 for giving the t and df each, giving 1 mark]

ANOVA

```
plot(time~treatment, data=minnows, ylab="time (secs)")
```



a) One Way ANOVA [30% marks - 6 marks]

SS_Residuals = 4928.0 - 1478.8 = 3449.2

df_treatment = k - 1 = 3 -1 = 2

df_residuals = df_tot - df_treatment = 33 - 2 = 31

MS_treatment = 1478.8 / 2 = 739.40

MS_residuals = 3449.2 / 31 = 111.26

F = 739.40 / 111.26 = 6.65

[0.5 marks for each category (the two df count as one category, and so do the two MS), 4 marks total]

(confirm in R)

```
minnows_lm<-lm(time~treatment,data=minnows)
anova(minnows_lm)
```

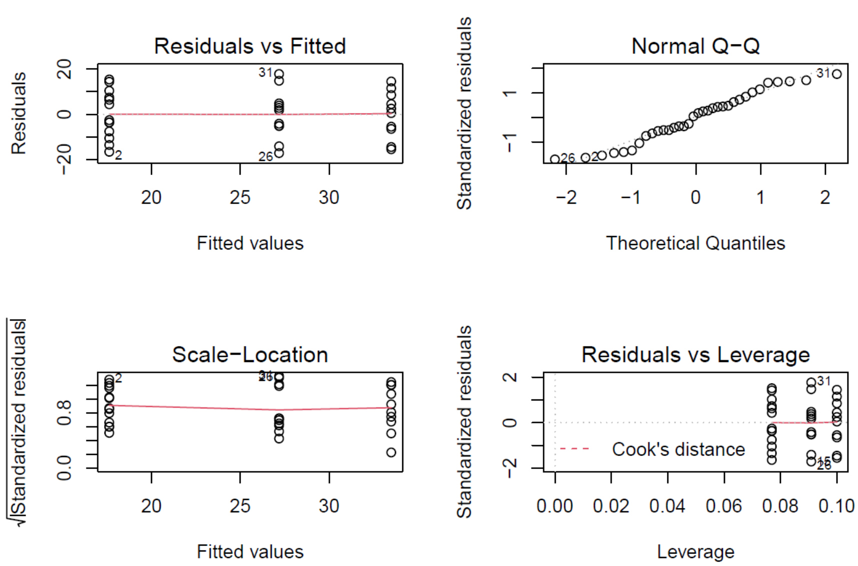
```
## Analysis of Variance Table
##
## Response: time
##           Df Sum Sq Mean Sq F value   Pr(>F)
## treatment  2 1478.8  739.41  6.6455 0.003965 **
## Residuals 31 3449.2  111.26
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

As the estimated F is larged than the critical value for $F_{2,31}$ (approx 3.32, for 2,30 df in table), the effect of turbidity is significant

[2 mark for reaching the correct conclusion]

d) Diagnostic plot [~15% marks 3 marks]

```
par(mfrow=c(2,2))
plot(minnows_lm)
```



All assumptiosn are generally well supported. Equality of variance is supported by the LHS plots. Normal Q-Q plot seems reasonable, even though some students might comment that there is a little bit snaking (that woudl be an acceptable concern).

[3 points]

e) Posthoc test [20% marks 4 marks]

```
TukeyHSD(aov(time~treatment,data=minnows))
```

```
##   Tukey multiple comparisons of means
##     95% family-wise confidence level
##
## Fit: aov(formula = time ~ treatment, data = minnows)
##
## $treatment
```

```
##                         diff       lwr      upr     p adj
## semiturbid-clear   9.566434 -1.069160 20.20203 0.0845575
## turbid-clear      15.884615  4.964773 26.80446 0.0032219
## turbid-semiturbid  6.318182 -5.025066 17.66143 0.3681720
```

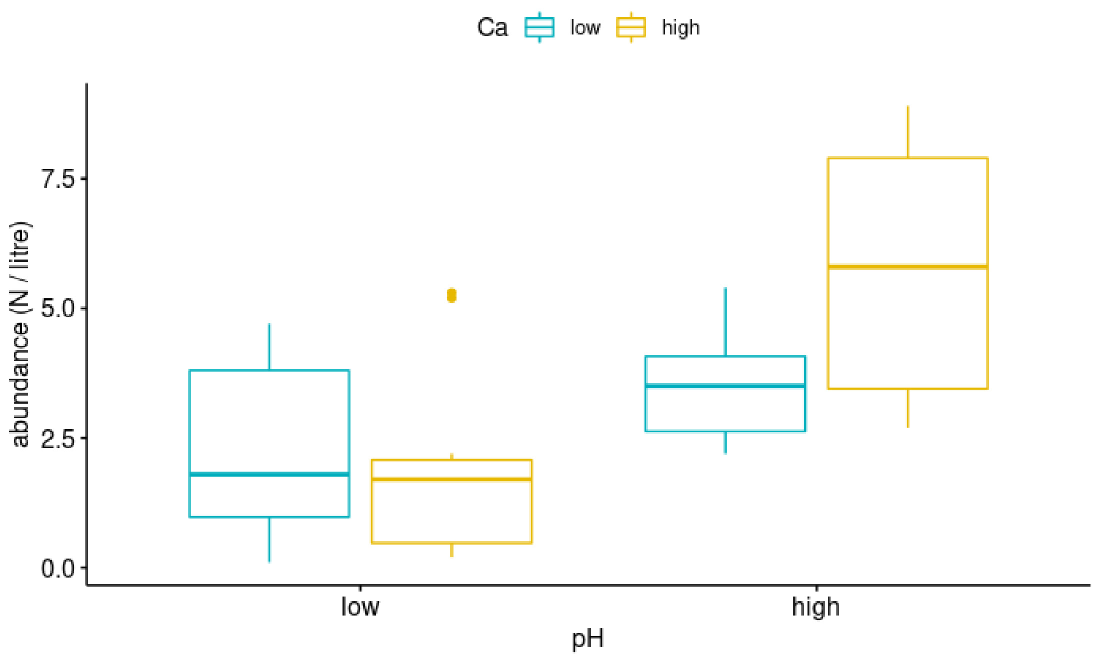
Only the second test is significant (0 not included in the 95%CI), the other two are not significant.

Turbidity affected the time taken by minnows to leave cover ($F_{2,31}$=6.65, $p<0.05$): minnows came out fastest in clear water and slowest in turbid water (Tukey's HSD $p<0.05$), with semiturbid water having an intermediate effect (not significantly different from clear or turbid based on Tukey's HSD $p>0.05$).

A good answer will give the omibus result (1 point), describe the effects (1 point), and realise that semiturbid is intermediate as it is not different from either of the two extremes (2 points).

B4

(a) An ecologist wants to study the impact of lake acidification, resulting from industrial pollution, on the abundance of zooplankton. Lakes that have been polluted for long periods of time also suffer a loss of calcium (Ca), which by itself might affect zooplankton. To disentangle the effect of acidity (pH) and Ca concentration, the ecologist sets up a number of microcosms which have a combination of high (alkaline) or low pH (acid), and low or high Ca concentration (10 for each combination of treatment levels). After one week, he estimates the mean number of zooplankton per litre (N / litre) in each mesocosm:



He fits a linear model of the interaction between the two predictors, and compares it with an additive model:

	Res. Df	**RSS**	**Df**	**SS**	**F**
Additive	37	135.95			
Interaction	**??**	119.05	1	**??**	**??**

Complete the table (i.e. the cells with the symbol **??**). Is the interaction significant? (show your work)

[~20% marks]

(b) Based on the coefficients from the model with interaction:

```
Call: lm(formula = abundance ~ pH + Ca + pH:Ca, data = zooplankton)
Coefficients:
  (Intercept)         pHhigh         Cahigh  pHhigh:Cahigh
         2.28           1.18          -0.33           2.60
```

what would you predict as the mean number of zooplankton for a mesocosm with low pH and high Ca? And for one with high pH and high Ca?

[~10% marks]

(c) The ecologist also attempts to drop the individual factors from the additive model:

	Res. Df	RSS	Df	SS	F
- Ca	38	145.35			
Additive	37	**??**	**??**	9.40	**??**

	Res. Df	RSS	Df	SS	F
- pH	38	197.45			
Additive	37	135.95	**??**	**??**	**??**

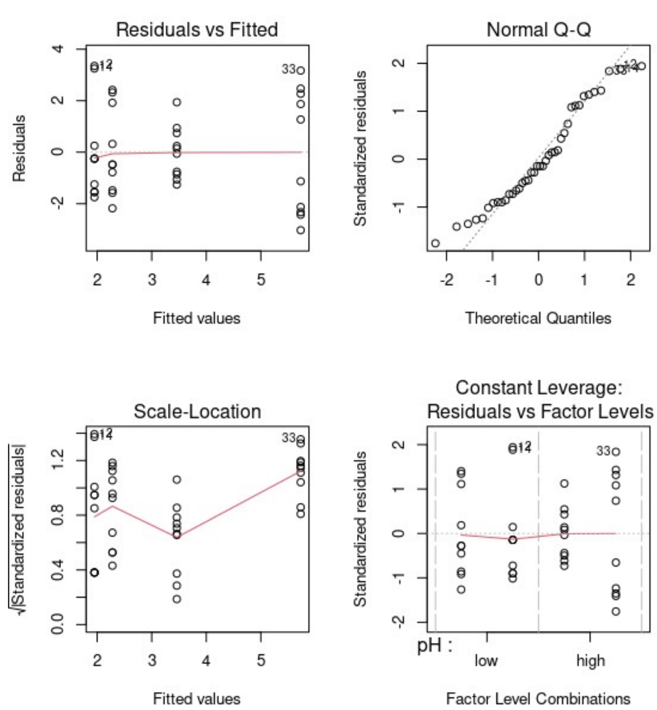
Complete the tables (i.e. the cells with the symbol **??**). Showing your work, what would you conclude from each of these drops? Was this step warranted?

[~30% marks]

(d) Provide a sentence that you could use to report the results in a scientific paper.

[~20% marks]

(e) What would you conclude from the diagnostic plots he obtained?

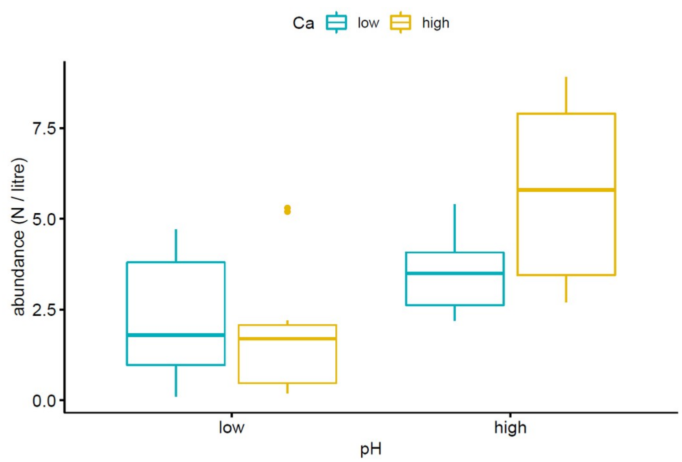


[~15% marks]

```
library("ggpubr")
```

```
## Loading required package: ggplot2
```

```
ggboxplot(zooplankton, x = "pH", y = "abundance", color = "Ca",
          palette = c("#00AFBB", "#E7B800"),ylab="abundance (N / litre)")
```



a) [20% marks - 4 marks]

Complete the table:

Df_inter = 37 - 1 = 36

SS_Delta = 135.95 - 119.05 = 16.9

MS_Delta = 16.9 / 1 = 16.9

MS_Resid = 119.05 / 36 = 3.3

F = 16.9 / 3.3 = 5.12

[0.5 mark per estimate for a total of 2.5 marks]

The estimated F is smaller the critical value for F 1,36 (between 4.17 and 4.08 from the table), so the interaction is significant.

[0.5 mark for comparing to the correct reference (correct df, etc.), and 1 mark for reaching the correct conlusion (i.e. a significant interaction)]

(Confirm it in R)

```
zoo_lm_inter<-lm(abundance~pH+Ca+pH:Ca,data=zooplankton)
zoo_lm_add<-lm(abundance~pH+Ca,data=zooplankton)
anova(zoo_lm_add,zoo_lm_inter)
```

```
## Analysis of Variance Table
##
## Model 1: abundance ~ pH + Ca
## Model 2: abundance ~ pH + Ca + pH:Ca
##   Res.Df    RSS Df Sum of Sq      F  Pr(>F)
## 1     37 135.95
## 2     36 119.05  1      16.9 5.1106 0.02992 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

b)[10% marks - 2 marks]

low_pH_high_Ca = 2.28 - 0.33 = 1.95

high_pH_high_Ca = 2.28 + 1.18 - 0.33 + 2.60 = 5.73

[1 mark per estimate]

c) Dropping main effects [35% marks - 7 points]

Dropping Ca

RSS_additive = 145.35 - 9.40 = 135.95

df_delta = 38 - 37 = 1

MS_delta = 9.40/1 = 9.40

MS_res = 135.95 / 37 = 3.67

F = 9.40 / 3.67 = 2.56

[0.5 marks per estimate for a total of 2.5 marks]

(test this in R)

```
zoo_lm_drop_Ca<-update(zoo_lm_add,.~.-Ca)
anova(zoo_lm_drop_Ca,zoo_lm_add)
```

```
## Analysis of Variance Table
##
## Model 1: abundance ~ pH
## Model 2: abundance ~ pH + Ca
##   Res.Df    RSS Df Sum of Sq      F Pr(>F)
## 1     38 145.35
## 2     37 135.95  1     9.409 2.5608  0.118
```

Dropping pH

df_delta = 38 - 37 = 1

SS_delta = 197.45 - 135.95 = 61.5

MS_delta = 61.5 / 1 = 61.5

MS_resid = 135.95 / 37 = 3.67

F = 61.5 / 3.67 = 16.76

[0.5 mark per estimate for a total of 2.5 marks]

```
zoo_lm_drop_pH<-update(zoo_lm_add,.~.-pH)
anova(zoo_lm_drop_pH,zoo_lm_add)
```

```
## Analysis of Variance Table
##
## Model 1: abundance ~ Ca
## Model 2: abundance ~ pH + Ca
##   Res.Df    RSS Df Sum of Sq      F    Pr(>F)
## 1     38 197.45
## 2     37 135.95  1    61.504 16.739 0.0002226 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

F_est is smaller than the critical value (F1,37 is between 4.17 and 4.08 from the table) for dropping Ca (i.e. not significant) but larger for pH (i.e. significant).

[0.5 for reaching correct conclusion for each test, for a total of 1 mark]

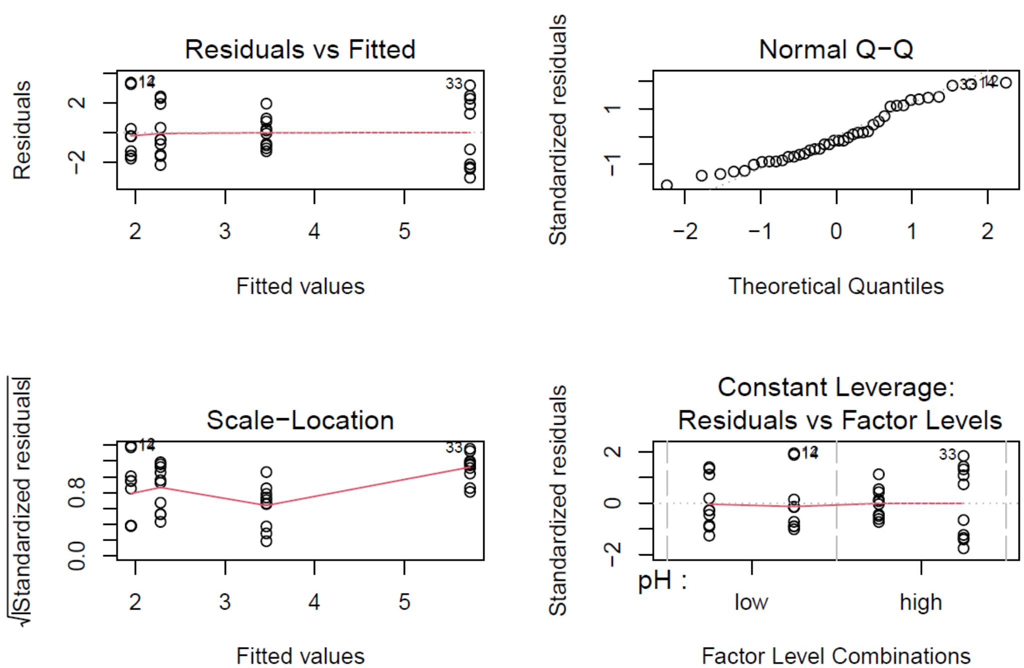
However, since the interaction was significant, he should not try to drop the main effects. [1 mark for correctly noting that the drops should not be considered with a significant interaction]

d) Sentence for paper [20% mark - 4 marks]

pH and Calcium levels interacted in their effect on zooplankton abundance ($F_{1,37}=16.76$, $p<0.05$): low pH were associated witht the lowest abundance, irrespective of the Ca level; at high pH, the largest abundanc was found at high Ca, with abundances for low Ca at an intermediate.

[0.5 mark for correct stats, df, and p value, 1 mark for saying there is a significant interaction, and 1.5 marks for describing the interaction.]

e) diagnostic plots [15% marks - 3 marks]



The assumption of equality of variance is not well supported, with the third group showing a smaller variance and the foruth showing a larger variance than the initial two groups (seen in the top and bottom left plots, 2 marks). Normal Q-Q plot shows some snaking close to the edges, especially for negative residuals (1 mark).

SECTION C

C5

The Richards' model can be used to represent plant disease epidemics. One way of writing that model assumes that $p(t)$, the proportion of infected plants at time t, is given by

$$\frac{dp}{dt}=\left(\frac{a}{b}\right)p\left(1-p^{b}\right),$$

in which a and b are positive constants. The initial proportion of infected plants is p_0.

(a) Show that the substitution $q=1/p^{b}$ can be used to transform the model into the linear differential equation

$$\frac{dq}{dt}=a(1-q).$$

[~20% marks]

(b) Solve this differential equation for $q(t)$ and use your solution to find $p(t)$.

[~20% marks]

(c) Verify that your solution for $p(t)$ is correct.

[~25% marks]

(d) For which proportion of infected plants is the epidemic size increasing most rapidly?

[~15% marks]

(e) Find equilibrium value(s) of p in the Richards' model and investigate whether the equilibrium value(s) are stable or unstable.

[~20% marks]

C5 sample answer:

(a)

The transformation indicates $p^b = q^{-1}$ and $p = q^{\frac{-1}{b}}$, which means

$$\frac{dp}{dt} = \frac{-1}{b} q^{-\left(\frac{1}{b}+1\right)} \frac{dq}{dt}$$

Replacing terms in the original equation

$$\frac{-1}{b} q^{-\left(\frac{1}{b}+1\right)} \frac{dq}{dt} = \left(\frac{a}{b}\right) q^{\frac{-1}{b}} - \left(\frac{a}{b}\right) q^{-\left(\frac{1}{b}+1\right)}$$

and so rearranging

$$\frac{dq}{dt} = -a q^{\frac{-1}{b}} q^{+\left(\frac{1}{b}+1\right)} + a = a(1-q)$$

(b)

The linearised equation is to be solved subject to $q(0) = 1/p_0^b$.

Separating the variables and integrating

$$\int \frac{1}{1-q} dp = \int a\, dt$$

and so

$$-\log(1-q) = at + C$$

The constant of integration, C, is

$$C = -\log\left(1 - 1/p_0^b\right)$$

and so

$$\log\left(\frac{1-1/p_0^b}{1-q}\right) = at$$

which means

$$\left(1-1/p_0^b\right) e^{-at} = 1-q$$

and so

$$q = 1 - J e^{-at}$$

where

$$J = \left(1 - 1/p_0^b\right)$$

The solution is therefore

$$p = \frac{1}{\left(1 - J e^{-at}\right)^{\frac{1}{b}}}$$

(c)

First note that when $t=0$,

$$p(0)=\frac{1}{(1-J)^{\frac{1}{b}}}=\frac{1}{\left(1-\left(1-\frac{1}{p_0^b}\right)\right)^{\frac{1}{b}}}=\frac{1}{\left(\frac{1}{p_0^b}\right)^{\frac{1}{b}}}=\frac{1}{1/p_0}=p_0$$

Left-hand side

$$\frac{dp}{dt}=\frac{d}{dt}\left[(1-Je^{-at})^{\frac{-1}{b}}\right]=-\left(\frac{1}{b}\right)(1-Je^{-at})^{-\left(\frac{1}{b}+1\right)}aJe^{-at}$$

Right-hand side

$$\left(\frac{a}{b}\right)p(1-p^b)=\left(\frac{a}{b}\right)\left(\frac{1}{(1-Je^{-at})^{\frac{1}{b}}}\right)\left(1-\frac{1}{(1-Je^{-at})}\right)$$

We can show that the two expressions are equal; for example, manipulating the right-hand side

$$\left(\frac{a}{b}\right)p(1-p^b)=\left(\frac{a}{b}\right)\left(\frac{1}{(1-Je^{-at})^{\frac{1}{b}}}\right)\left(\frac{-Je^{-at}}{(1-Je^{-at})}\right)\text{¿}-\left(\frac{a}{b}\right)\left(\frac{Je^{-at}}{(1-Je^{-at})^{\left(\frac{1}{b}+1\right)}}\right)$$

(d)

To find an expression for d^2p/dt^2

$$\frac{d^2p}{dt^2}=\left(\frac{a}{b}\right)\frac{d}{dt}\left(p(1-p^b)\right)=\left(\frac{a}{b}\right)\frac{dp}{dt}\frac{d}{dp}\left(p-p^{b+1}\right)=\left(\frac{a}{b}\right)\frac{dp}{dt}\left(1-(b+1)p^b\right)$$

The epidemic grows fastest if $p=\left(\frac{1}{b+1}\right)^{1/b}$

(You might also tackle this by differentiating the expression for p twice with respect to time)

C6

A population of the eastern spruce budworm, *Choristoneura fumiferana*, is modelled via

$$\frac{dB}{dt} = f(B) = rB,$$

in which $B(t)$ is the population size at time t and r is a positive constant.

(a) If the initial population size is B_0, solve the model to find $B(t)$

[~10% marks]

Budworms can be eaten by birds. The bird population is assumed to remain constant, meaning the net rate of predation can be modelled as

$$g(B) = \frac{pB^2}{a^2 + B^2},$$

in which a and p are constant parameters and where the numerical value of p would depend on the (fixed) size of the bird population.

(b) Find dg/dB and d^2g/dB^2, and verify that $d^2g/dB^2 = 0$when $g(B) = p/4$.

[~20% marks]

(c) Sketch $g(B)$ as a function of B (for $B \geq 0$¿.

[~10% marks]

The model of the budworm population is updated to include predation by the bird population

$$\frac{dB}{dt} = f(B) - g(B) = rB - \frac{pB^2}{a^2 + B^2}.$$

(d) Show that the updated model has an equilibrium when $B = 0$, as well as up to two further equilibria given by solutions to the quadratic equation

$$B^2 - \left(\frac{p}{r}\right)B + a^2 = 0.$$

[~10% marks]

(e) Show that if $p > 2ar$ the quadratic has two positive solutions.

[~10% marks]

For the remainder of this question, you should assume that $p > 2ar$.

(f) Sketch a graph of dB/dt as a function of B.

[~15% marks]

(g) Sketch representative graphs of B as a function of t, showing behaviour for different initial sizes of the budworm population.

[~10% marks]

(h) Comment upon how the results of this model might be unrealistic for large times and suggest two distinct alterations to the model to mitigate this lack of realism.

[~15% marks]

C6 solution

(a)

Separating the variables

$$\int \frac{1}{B} dB = r \int dt$$

which means

$$\log(B) = rt + C$$

The initial condition means

$$C = \log(B_0)$$

and so

$$B = B_0 e^{rt}$$

(b)

Via the quotient rule

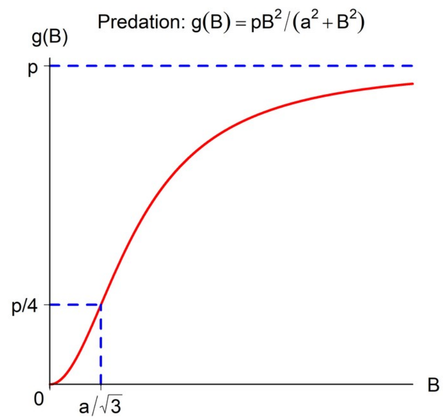
$$\frac{dg}{dB} = \frac{(a^2 + B^2) 2pB - pB^2 2B}{(a^2 + B^2)^2} = \frac{2pa^2 B}{(a^2 + B^2)^2}$$

Differentiating again

$$\frac{d^2 g}{d B^2} = \frac{\left(a^2+B^2\right)^2 2 p a^2 - 2 p a^2 B \left(2\left(a^2+B^2\right) 2 B\right)}{\left(a^2+B^2\right)^4} = \left(\frac{2 p a^2}{\left(a^2+B^2\right)^3}\right)\left(a^2-3 B^2\right)$$

Note that $d^2 g / d B^2 = 0$ when $a^2 = 3 B^2$, and so $g(B) = p/4$

(c)



Curve is non-negative for all B

Sigmoid, with inflexion point (at $p/4$¿ [labelled on sketch]

$g \rightarrow p$ as $B \rightarrow \infty$ [labelled on sketch]

Curve is flat as $B \rightarrow 0$

(d)

At equilibrium $dB/dt = 0$, i.e.

$$B\left(r - \frac{pB}{a^2+B^2}\right) = 0$$

This means there is one equilibrium when $B = 0$

Other equilibria follow from roots of

$$r\left(a^2+B^2\right) - pB = 0$$

i.e.

$$B^2 - \left(\frac{p}{r}\right) B + a^2 = 0$$

(e)

The quadratic has two roots at

$$B_{\pm}=\frac{\frac{p}{r}\pm\sqrt{\left(\frac{p}{r}\right)^2-4a^2}}{2}$$

Note that because $4a^2>0$,the quantity inside the square root must be less than $\left(\frac{p}{r}\right)^2$, and so if two roots exist, both must be positive

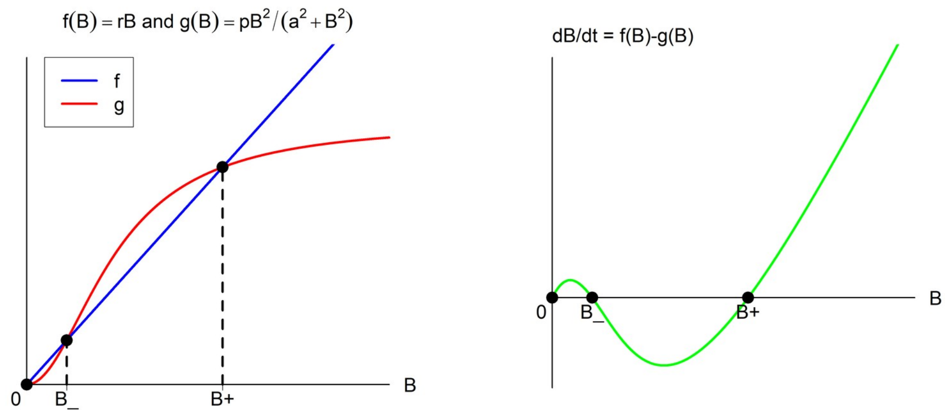
So we are really being asked about a condition for two roots to exist, i.e.

$$\left(\frac{p}{r}\right)^2-4a^2>0$$

$$p>\sqrt{4a^2r^2}=2ar$$

(Other ways of justifying this, e.g. algebraically, or perhaps by analogy with stability of 2D linear systems)

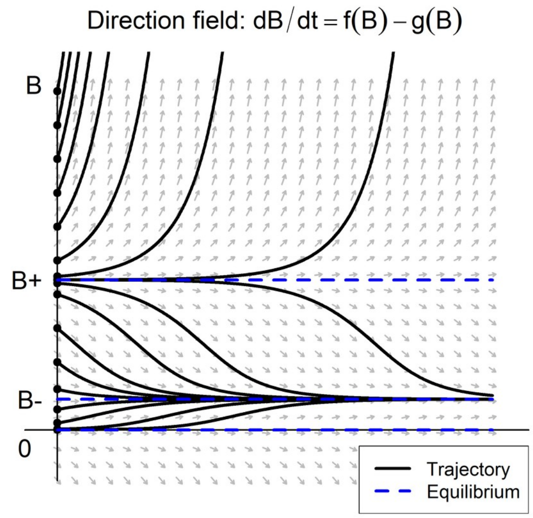
(f)



Two positive equilibria, and one at zero.

Correct sign for $0<B<B_{-¿¿}$ (positive); $B_{¿}¿$ (negative); $B_{+¿<B¿}$(positive)

(g)



Low initial populations lead to population being attracted to $B_{-¿¿}$

Same for populations starting above $B_{-¿¿}$ but below $B_{+¿¿}$, which will decrease to $B_{-¿¿}$

But if population starts above $B_{+¿¿}$ then $B \to \infty$

A convincing answer might show at least one inflexion point somewhere (can be on either the increasing or decreasing solution curves which tend to an equilibrium).

(h)

Irrespective of parameters chosen, $B \to \infty$ as $t \to \infty$ if initial budworm population is too large (no need to note too large; just noting that the population eventually explodes for “some” initial conditions is enough).

Alter $f(B)$ such that growth of the budworm population is bounded, e.g. logistic growth.

Allow the size of the bird population to affect p in response to any increase in B.

SECTION D

D7

For the non-linear system of equations given by:

$$\frac{dx}{dt} = x^2 + y^2 - 4$$

$$\frac{dy}{dt} = x^2 + xy$$

(a) Find and classify all equilibria.

[~30% marks]

(b) Sketch the phase plane, marking on clearly the nullclines, equilibrium points, direction field and sufficient trajectories to illustrate the behaviour of the system.

[Note: all sketches should be drawn on a blank page by hand, not by using a computer to create a plot for you.]

[~30% marks]

(c) Consider the two pairs of initial conditions $(x$¿¿$0, y_0) = (-1, -2)$¿ and $(x$¿¿$0, y_0) = (-1, -2.5)$¿. Mark clearly the trajectories associated with these two initial conditions on the phase plane. Do these two trajectories correspond to solutions with the same long-term behaviour? Justify your answer using the direction field and location of nullclines.

[~20% marks]

(d) For the initial condition $(x$¿¿$0, y_0) = (-1, -2.5)$¿, sketch the graphs for $x(t)$ and $y(t)$ on the same set of axes.

[~20% marks]

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D7

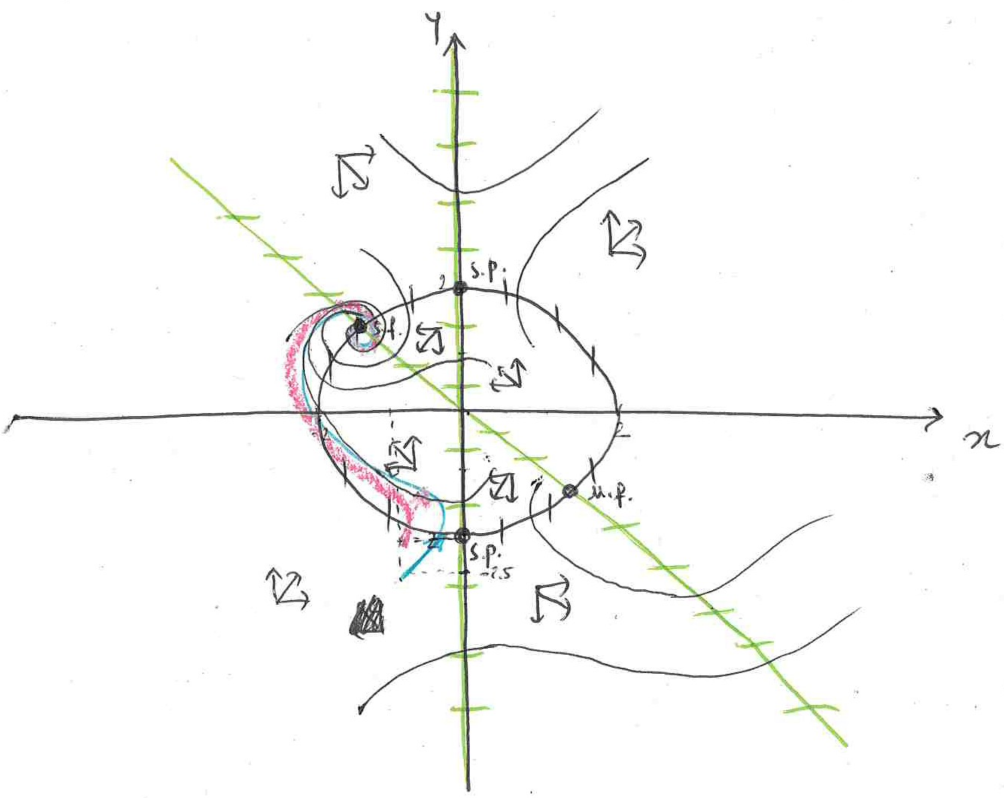
a) $\begin{cases} x^2+y^2-4=0 & (1) \\ x(x+y)=0 \end{cases} \Leftrightarrow \begin{cases} \text{—} \\ \underset{(2a)}{x=0} \quad \text{or} \quad \underset{(2b)}{y=-x} \end{cases}$

- (1) + (2a) : $\quad y^2-4=0$
  $\underline{x=0}$ $\qquad y^2=4 \quad \Rightarrow \quad (0,2)$
  $\qquad y=\pm 2 \qquad (0,-2)$

- (1) + (2b) : $\quad x^2+(-x)^2-4=0$
  $\underline{y=-x}$ $\qquad 2x^2=4$
  $\qquad x^2=2 \qquad (\sqrt{2},-\sqrt{2})$
  $\qquad x=\pm\sqrt{2} \quad \Rightarrow \quad (-\sqrt{2},\sqrt{2})$

		$(0,2)$	$(0,-2)$	$(\sqrt{2},-\sqrt{2})$	$(-\sqrt{2},\sqrt{2})$
D_{11}	$2x$	0	0	$2\sqrt{2}$	$-2\sqrt{2}$
D_{12}	$2y$	4	-4	$-2\sqrt{2}$	$2\sqrt{2}$
D_{21}	$2x+y$	2	-2	$2\sqrt{2}-\sqrt{2}=\sqrt{2}$	$-2\sqrt{2}+\sqrt{2}=-\sqrt{2}$
D_{22}	x	0	0	$\sqrt{2}$	$-\sqrt{2}$
T		0	0	$3\sqrt{2}>0$	$-3\sqrt{2}<0$
Δ		$0-8=-8<0$	$0-8=-8<0$	<u>unstable</u>	<u>stable</u>
$T^2-4\Delta$		<u>saddle point</u>	<u>saddle point</u>	$(3\sqrt{2})^2-4(8)=18-32=-14$ <u>focus</u>	$(-3\sqrt{2})^2-4(8)=18-32=-14$ <u>focus</u>

b)



@ $(x,y)=(1,1)$:

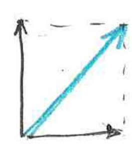
$$x' = 1^2+1^2-4 = 2-4 = -2 < 0$$
$$y' = 1(1+1) = 2 > 0$$

c) @ $(x_0,y_0)=(-1,-2)$

$$x' = (-1)^2+(-2)^2-4 = 1+4-4 = 1$$
$$y' = (-1)(-1-2) = -1(-3) = 3$$

@ $(x_0,y_0) = (-1,-2.5)$

$$x' = (-1)^2+(-2.5)^2-4 = 1+6.25-4 = 3.25$$
$$y' = (-1)(-1-2.5) = 3.5$$



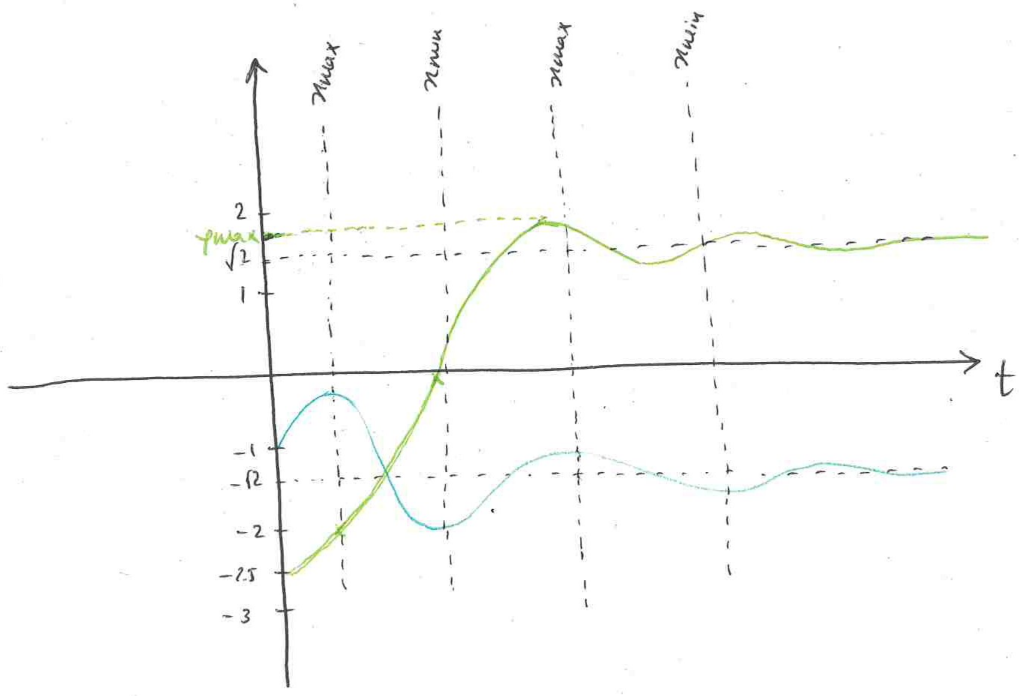
c) (continued)

Yes, both trajectories correspond to solutions with the same long term behaviour.

For $(x_0, y_0) = (-1, -2)$ the initial direction field is $(x'_0, y'_0) = (1, 3)$ and the starting point is also closer to the x-cline $x^2+y^2-4=0$. Therefore this trajectory will move upwards until it crosses the x-cline. After that the trajectory is 'captured' by the stable focus, leading to $x \to -\sqrt{2}$ and $y \to \sqrt{2}$ when $t \to +\infty$.

The trajectory for $(x_0, y_0) = (-1, -2.5)$ needs more careful consideration to decide whether it will cross the x-cline $x^2+y^2-4=0$ or the y-cline $x=0$. The starting direction field is $(x', y') = (3.25, 3.5)$ so the trajectory starts of at an angle of approximately $45°$, which means it is moving towards positive y values and positive x values at approximately equal rates. However, because the starting point is slightly closer to the x-cline than the y-cline $x=0$, and therefore it is more likely that this trajectory will cross the x-cline $x^2+y^2-4=0$, before it reaches the y-cline $x=0$.

d)



D8

This question models the joint dynamics of plants in a meadow, with density $V(t)$, and aphids, with density $A(t)$, that feed on the plants.

$$\frac{dV}{dt}=rV\left(\frac{1}{1+A}-\frac{V}{k}\right)$$

$$\frac{dA}{dt}=\alpha V A-\mu A$$

You can assume that all parameters are positive $(r>0, k>0, \alpha>0, \mu>0)$.

(a) In the absence of aphids, what type of growth do the plants follow and what do parameters r and k represent?

[~15% marks]

(b) Calculate the null-clines and stationary points of the system and show that aphids can only persist if $k>\mu/\alpha$.

[~40% marks]

(c) Prove the stability of a coexistence equilibrium when $k>\mu/\alpha$.

[~30% marks]

(d) Sketch the two possible configurations of the phase plot, including the direction fields.

[~15% marks]

Sample answers for D8:

a. Logistic growth, with intrinsic growth rate r and carrying capacity k.

b. V nullclines: solve dV/dt=0. Two solutions : $V=0$ or $A=\frac{k}{V}-1$.

(The second nullcine can also be written as $V=\frac{k}{1+A}$).

A nullcines: solve dA/dt. Two solutions : $A=0$ or $V=\mu/\alpha$.

There are three stationary points:
$V=0, A=0$
$V=k, A=0$
$V=\frac{\mu}{\alpha}, A=\frac{k\alpha}{\mu}-1$
The third one represents coexistence and is only feasible (A>0) if $k>\mu/\alpha$.

c. In this question we assume $k>\mu/\alpha$. Let

$$F(V,A)=rV\left(\frac{1}{1+A}-\frac{V}{k}\right)$$

$$\frac{\partial F}{\partial V}=\frac{r}{1+A}-\frac{2rV}{k}, \frac{\partial F}{\partial A}=\frac{-rV}{(1+A)^2}[2]$$

$$G(V,A)=\alpha V A-\mu A$$

$$\frac{\partial G}{\partial V}=\alpha A, \frac{\partial G}{\partial A}=\alpha V-\mu[2]$$

Then substitute $V=\frac{\mu}{\alpha}, A=\frac{k\alpha}{\mu}-1$ which we can rewrite as $\frac{1}{1+A}=\frac{\mu}{k\alpha}$.

Coefficient matrix:

$$\begin{pmatrix} \frac{-r\mu}{k\alpha} & \frac{-r\mu^3}{k^2\alpha^3} \\ \alpha\left(\frac{k\alpha}{\mu}-1\right) & 0 \end{pmatrix}$$

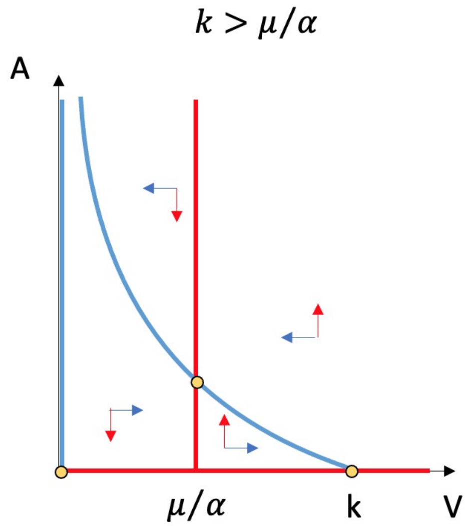
With trace $T=\frac{-r\mu}{k\alpha}<0$

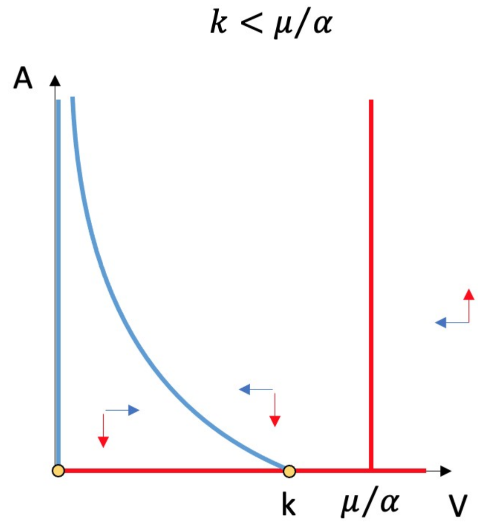
and determinant $\Delta=\frac{r\mu^2}{k^2\alpha^2}(k\alpha-\mu)>0$.

Hence the coexistence stationary point is stable.

d. Direction field: near the origin: $dV/dt \approx rV > 0$ and $\frac{dA}{dt} \approx -\mu A < 0$.

Phase plots (V nullclines in blue, A nullclines in red):





SECTION E

E9

The following scheme describes a simplified mechanism for mixed inhibition of an enzyme catalysed reaction, in which the enzyme, E, facilitates the conversion of a single substrate, S, into a product, P, via the formation of an enzyme-substrate complex, ES. The inhibitor, I, can interact with both free enzyme E and the ES complex.

$$\begin{array}{ccccc} \mathrm{E + S + I} & \underset{k_2}{\overset{k_1}{\rightleftharpoons}} & \mathrm{ES + I} & \xrightarrow{k_3} & \mathrm{E + P + I} \\ k_5 \Big\uparrow\Big\downarrow k_4 & & k_7 \Big\uparrow\Big\downarrow k_6 & & \\ \mathrm{EI + S} & & \mathrm{EIS} & & \end{array}$$

(a) Construct a molar balance equation for the total concentration of enzyme that is present at time zero, $[E]_0$.

[~5% marks]

(b) Write down two differential equations that describe how the rates of change of [ES] and [P] vary as a function of time, *t*.

[~10% marks]

(c) If

$$K_8 = \frac{[E][S]}{[ES]} = \frac{k_2 + k_3}{k_1}, \quad K_9 = \frac{[E][I]}{[EI]} = \frac{k_5}{k_4} \quad \text{and} \quad K_{10} = \frac{[ES][I]}{[ESI]} = \frac{k_7}{k_6},$$

apply the steady state approximation to the enzyme-substrate complex and construct an expression for [ES] in terms of constants and the current concentrations of free enzyme, [E], and free substrate, [S].

[~10% marks]

(d) Next, construct expressions for [EI] and [ESI] in terms of constants and the current concentrations of free enzyme, [E], free substrate, [S], and free inhibitor, [I].

[~10% marks]

(e) Construct an expression for the current concentration of free enzyme [E] in terms of constants and the current concentrations of free substrate, [S], and free inhibitor, [I].

[~10% marks]

(f) Construct an expression for the rate of change of product concentration, [P], in terms of constants and the current concentrations of free substrate, [S], and free inhibitor, [I].

[~10% marks]

(g) Use your results from part ***(f)*** to show that v_0, the initial rate of formation of product, obeys a rate law equation of the form:

$$v_0 = \frac{V_{MAX}'[S]_0}{K_M' + [S]_0}$$

where $[S]_0$ is the initial concentration of substrate. State any approximations you have made and explain how V_{MAX}' and K_M' depend on the values of other constants and the concentrations of specific species.

[~30% marks]

(h) Would you expect the value of V_{MAX}' to be larger or smaller than the value of V_{MAX} that would have been determined if no inhibitor had been present? Explain your answer.

[~5% marks]

(i) If enzyme E acts in the middle of a metabolic pathway and the purpose of inhibiting it is to reduce the rate of production of product P, explain what advantage there might be in using an inhibitor with mixed characteristics over one that possesses purely competitive characteristics.

[~10% marks]

Sample answers for E9:

(a) $[E]_0 = [E] + [ES] + [EI] + [ESI]$

(b) $d[ES]/dt = + k_1[E][S] - (k_2 + k_3)[ES] - k_6[ES][I] + k_7[ESI]$

$d[P]/dt = +k_3[ES]$

(c) $0 = d[ES]/dt = + k_1[E][S] - (k_2 + k_3)[ES] - k_6[ES][I] + k_7[ESI]$

But $K_{10} = [ES][I]/[ESI] = k_7/k_6$,

so $k_6[ES][I] = k_7[ESI]$

so $k_1[E][S] - (k_2 + k_3)[ES] = 0$

i.e. $[ES] = [E][S].k_1/(k_2 + k_3) = [E][S]/K_8$

(d) Since $K_9 = [E][I]/[EI]$, $[EI] = [E][I]/K_9$

And since $K_{10} = [ES][I]/[ESI]$, $[ESI] = [ES][I]/K_{10} = [E][S][I]/(K_8K_{10})$

(e) $[E]_0 = [E] + [ES] + [EI] + [ESI]$

$= [E] + [E][S]/K_8 + [E][I]/K_9 + [E][S][I]/(K_8K_{10})$

$= [E](1 + [S]/K_8 + [I]/K_9 + [S][I]/(K_8K_{10}))$

Therefore $[E] = [E]_0/(1 + [S]/K_8 + [I]/K_9 + [S][I]/(K_8K_{10}))$

(f) $d[P]/dt = k_3[ES] = k_3[E][S]/K_8 = k_3[E]_0[S]/(K_8(1 + [S]/K_8 + [I]/K_9 + [S][I]/(K_8K_{10}))$

i.e. $d[P]/dt = k_3[E]_0[S]/(K_8 + [S] + [I]K_8/K_9 + [S][I]/K_{10})$

(g) Under initial rate conditions, we can assume that $[S] = [S]_0$ and $[I] = [I]_0$

Therefore $v_0 = k_3[E]_0[S]_0/(K_8 + [S]_0 + [I]_0K_8/K_9 + [S]_0[I]_0/K_{10})$

i.e. $v_0 = k_3[E]_0[S]_0/(K_8(1 + [I]_0/K_9) + [S]_0(1 + [I]_0/K_{10}))$

$= (k_3[E]_0/(1 + [I]_0/K_{10})).[S]_0/(K_8(1 + [I]_0/K_9)/(1 + [I]_0/K_{10}) + [S]_0)$

$= V_{MAX}'[S]_0/(K_M' + [S]_0)$

with $V_{MAX}' = k_3[E]_0/(1 + [I]_0/K_{10})$

and $K_M' = K_8(1 + [I]_0/K_9)/(1 + [I]_0/K_{10})$

(h) Since $V_{MAX}' = k_3[E]_0/(1 + [I]_0/K_{10})$

and in the absence of inhibitor we would expect $V_{MAX} = k_3[E]_0$,

we would expect $V_{MAX}' < V_{MAX}$

because $[I]_0 > 0$, $K_{10} > 0$, and thus $[I]_0/K_{10} > 0$

(i) Competitive inhibition can be overcome by increasing the substrate concentration, meaning that if [S] can become high enough, the initial rate v_0 can reach a maximum value of V_{MAX}.

In a metabolic pathway, we might expect the concentration of substrate S to increase if enzyme E is inhibited, because its concentration is no longer being depleted by the reaction, and this increase in [S] might eventually become large enough to overcome inhibition by a competitive inhibitor.

For a mixed inhibitor we have discovered that the maximal rate at high substrate concentrations will be V_{MAX}', which is smaller than V_{MAX}.

If the purpose of using an inhibitor is to reduce the rate of production of product P, then this objective can be achieved by a mixed inhibitor even if the substrate concentration gets very high.

E10

A pair of birds can each visit either of two alternative foraging locations. Each bird prefers a different location, but both prefer to forage together (as they are more vulnerable to predation when alone). Thus each bird must decide whether to visit its own preferred site (referred to as 'Selfish' behaviour), or whether to visit the other's preferred site (referred to as 'Accommodating' behaviour). The matrix below shows the payoff to a bird, depending on its own choice of behaviour (listed down the left-hand side of the matrix) and that of the other (listed along the top of the matrix):

		Other's Behaviour:	
		Selfish	Accommodating
Own Behaviour:	Selfish	$2-k$	2
	Accommodating	$2-c$	$2-c-k$

This matrix is based on the assumption that each bird receives a baseline payoff of 2, but pays a cost of c if it visits its non-preferred site, and a cost of k if it ends up foraging alone (where $0 < c, k \leq 1$).

(a) Under what circumstances is each strategy evolutionarily stable?

[~15% marks]

(b) Determine the circumstances under which the game yields a mixed evolutionarily stable strategy (ESS). What is the frequency of Selfish behaviour at such an ESS?

[~35% marks]

(c) Use your results from part ***(b)*** to derive an expression for the probability that the two birds forage together at the mixed ESS.

[~25% marks]

(d) Use your results from part ***(b)*** to derive an expression for the mean payoff to a bird at the mixed ESS.

[~25% marks]

Sample answers for E10:

a)

Selfish strategy stable when W(A,S) ≤ W(S,S) (and if W(A,S) = W(S,S) then W(A,A) < W(S,A)):

$2-c \leq 2-k \Rightarrow k \leq c$ (and if $k = c$ then $2-c-k < 2$, which must be true since $0 < c,k \leq 1$)

Accommodating strategy stable when when W(S,A) ≤ W(A,A) (and if W(S,A) = W(A,A) then W(S,S) < W(A,S)):

$2 \leq 2-c-k$, never satisfied since $0 < c,k \leq 1$; so Accommodating strategy never stable

b) Mixed ESS when neither pure strategy stable, i.e. when $k > c$

Let s denote frequency of selfishness at such a mixed ESS. From Bishops-Canning theorem, payoffs to both behaviours must be equal at a mixed ESS, so

$s\, W(S,S) + (1-s)\, W(S,A) = s\, W(A,S) + (1-s)\, W(A,A)$

$s(2-k) + 2(1-s) = s(2-c) + (1-s)(2-c-k)$

$\Rightarrow 2 - sk = 2 - c - (1-s)k$

$\Rightarrow s = (k+c)/(2k)$

c) The two birds forage together at the mixed ESS if one is Selfish and the other Accommodating. This occurs with probability

$2s(1-s) = 2((k+c)/(2k)).((k-c)/(2k)) = (k^2-c^2)/(2k^2) = (1/2)(1-(c^2/k^2))$

d) Payoff at a mixed ESS is equal to

$s^2\, W(S,S) + s(1-s)\, W(S,A) + s(1-s)\, W(A,S) + (1-s)^2\, W(A,A)$

$= s^2\,(2-k) + s(1-s)\, 2 + s(1-s)(2-c) + (1-s)^2(2-c-k)$

$= 2 - (1-s)c - (1-2s(1-s))k$

Substituting into the above the value of s obtained in (b)

$= 2 - (1/2)c(1 - (c/k)) - (1/2)k(1 + (c^2/k^2)) = 2 - (1/2)c - (1/2)k$