Prifysgol Abertawe
Swansea University

Comparing the rate of weapon and ornament diversification

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Abstract

In some species in one sex, generally males, ornaments evolve to attract females and/or sexually selected weapons evolve as a response to intrasexual competition for mating opportunities. A key prediction of classic Darwin/Fisher/Lande sexual selection theory is that sexually selected ornaments should evolve faster than sexually selected weapons. As male ornaments and female preferences for particular ornamental traits coevolve, selection occurs in both males and females and a positive feedback loop potentially enhancing the rate of trait evolution can develop under the Fisher process (Fisherian runaway selection)In this thesis I measure the rate of trait evolution of many examples of weapons and ornaments to test this at a macroevolutionary scale. . I assembled data on weapon and ornament traits from 22 diverse animal taxa. Pairs of weapon and ornament datasets comprising closely related taxa were formed to control factors such as generation time that may influence the different rates between traits. Trait values were standardised and the rates were compared using recently developed phylogenetic analyses under both Brownian motion and Ornstein-Uhlenbeck evolutionary models. I found strong evidence under both models that ornaments have consistently evolved faster than weapons. This suggests that Fisherian runaway processes have broad influence on the evolution of sexually selected ornaments at macroevolutionary scales across diverse taxa.

Lay summary

Across the animal kingdom males are often observed with exaggerated physical traits. These generally are either to send a signal of fitness to females and are ornaments, or they are used during combat with males of the same species and are weapons. Some examples of ornaments are long tails or brightly coloured plumage in birds and the exaggerated neck flaps in lizards. Weapon examples include large horns in bovids, and beetles and long canines seen in carnivores and primates. The traits tend to be on a sliding scale of their function being a true weapon or a true ornament as weapons can act as a signal to both males and females of their fighting ability removing the need for combat in some cases such as the bovid horns.

The more exaggerated the weapon or ornament trait is the more natural selection will work against it. This is because the traits require more energy to create or to carry and make the individual more conspicuous to predators. An exaggerated trait can signal to the female that the male is fit, although female beauty aesthetics can be arbitrary and not related to fitness. The selection of ‘attractive’ traits can cause a feedback loop on the trait as sexual selection is a strong directional force speeding up the rate that the trait evolves. As this force of female choice is not acting upon the weapon traits it is expected that weapons will evolve slower than ornaments.

I collected weapon and ornament datasets from across the animal kingdom and paired them together based on how related the species were. I also created two datasets for this report to match with currently available datasets. As the traits were from a wide range of species and in multiple scales the datasets needed to be standardised to compare. Once standardised the rates of evolution were analysed under the evolutionary model Brownian motion and Ornstein-Uhlenbeck (figure x). The results show strong evidence for the key sexual selection theory of Fisherian runaway processes, which has not been demonstrated in a report with such diverse species before.

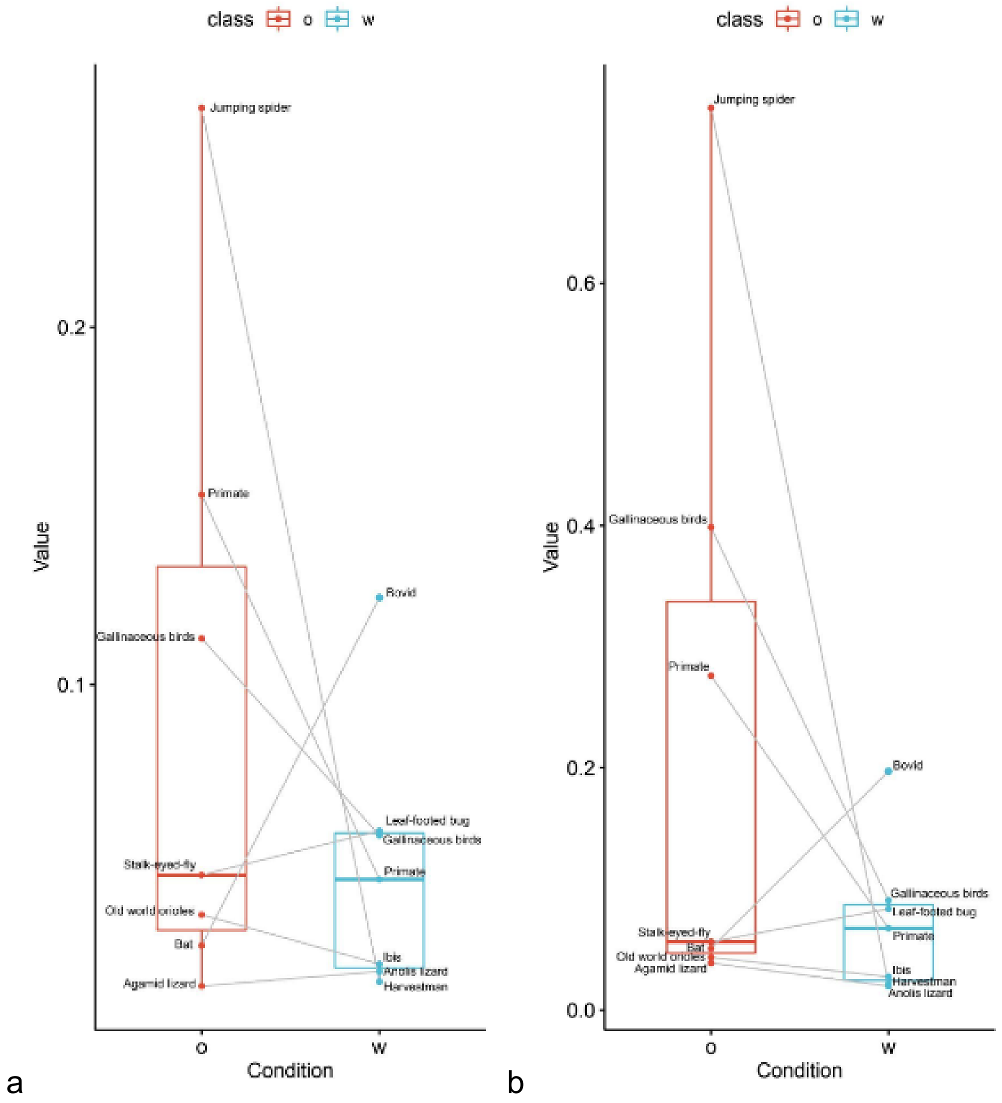

Figure X – In both plots ornaments are red and weapons are blue. Each point represents the evolutionary rate of trait dataset. a: The results of the ratebytree analysis using the BM model. b: The results of the ratebytree analysis using the OU model.

University Declarations and Statements

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed [redacted]

Date 28/09/2021

This work is the result of my own independent study/investigation, except where otherwise dated. Other sources are acknowledged by explicit references. A bibliography is appended.

Signed [redacted]

Date 28/09/2021

I hereby give my consent for my work, if relevant and accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed [redacted]

Date 28/09/2021

MRes Biosciences Statement of Expenditure

Student name: Megan Watts

Student number: [redacted]

Project title: Comparing the rates of ornament and weapon diversification

Category	Item	Description	Cost
N/A	N/A	N/A	N/A

I hereby certify that the above information is true and correct to the best of my knowledge.

[redacted]

Signature (Supervisor)

Signature (Student)

Statement of Contributions

Contributor Role	**Persons involved**
Conceptualisation	WA
Data curation	MW, WA, LH
Formal analysis	MW, WA
Funding acquisition	N/A
Investigation	MW
Methodology	WA, MW
Project administration	WA
Resources	WA
Software	WA, MW
Supervision	WA
Validation	N/A
Visualisation	MW, WA
Writing – original draft preparation	MW
Writing – review and editing	WA

MW = Megan Watts (Author)

WA = Will Allen (Supervisor)

LH = Louisa Hutton (Previous MRes candidate, Swansea University)

Contents

Acknowledgements

I would like to thank my supervisor, Dr Will Allen, for supporting me throughout the whole project and guiding me to the completion of this thesis.

Definitions and Abbreviations

BM = Brownian motion

OU = Ornstein-Uhlenbeck

EB = Early burst

PGLS = Phylogenetic generalised least squares

MDS = Multi-dimensional scaling

AIC = Akaike information criteria

Tables and Figures

Please note form is shown for 19/20. Any previously completed assessments can be accessed using the session links shown in the top right-h
page.

**Please complete self-assessment as accurately as possible. Once complete, ensure you have ticked the declaration box before submitting to your supervisor. If afte
errors in your self-assessment, to clear the error before starting new assessment please contact: Sridevi Kanamarlapudi**

Student Details

Name:	Megan Watts
Student Number:	[redacted]
Level:	7
Course:	Biosciences
Project Supervisor:	Dr William Allen
Last Updated Date:	27 Mar 2020, 10:55 a.m.
Last Reviewed Date:	27 Mar 2020, 11:01 a.m.
Reviewed by:	William Allen

Projects Ethics Assessment Status

Project Title	Status	Approval Number
Using acoustic camouflage to evade gleaning bats	Completed	SU-Ethics-Student-270320/2623
Comparing the rate of weapon and ornament diversifiaction	Completed	SU-Ethics-Student-270320/2738

Additional forms to be submitted as part of this assessment and their status(only Project Supervisor can submit additional forms to relevant Committee):

- Animal vertebrate review form(STU_BIOL_132249_290220155825_1) - Approved Proposal :College Ethics Committee DECISION Details

Additional ethical assessment(s)

Click 'Ethics Assessment for new project' to submit additional assessment(s) for this or other projects.

It is mandatory requirement to complete this Project Ethics Assessment before starting any project in the College. Any further assessme submitted as and when required. A unique reference number will be generated and sent to you by email for each of the completed Et Assessment below.

You will find useful documents at: Ethics Resources

Approval Number: SU-Ethics-Student-270320/2738

Reference Number: STU_BIOL_132249_270320105554_2

Status: Completed

Project Title: Comparing the rate of weapon and ornament diversifiaction

Project Start Date: 03/20

Project Duration: 6 months

Please respond to questions below as accurately as possible and tick the DECLARATION box at the end of the form before submitting to your supervisor.

Please answer only relevant questions as instructed below.

1. Have you read information within the University's Research Ethics and Governance Framework document that is relevant to your research?

☑ Yes. Go to 2

☐ No. **STOP.** You **cannot** begin your project without reading it. Then Go to 2.

2. Does the study make use of OR generate data?

☑ Yes. Go to 3

☐ No. Tick DECLARATION box and Save this form. You can begin your project once your supervisor has reviewed this assessment.

3. Does the study only make use of data which are already in the public domain?

☑ Yes. Tick DECLARATION box and Save this form. You can begin your project once your supervisor has reviewed this assessment.

☐ No. Go to 4

4. Does your study pose a potential risk to the environment, such as the escape of invasive species, genetically modified organisms (GMO), work involving huma pathogens, environmental contaminants, radioactive material or active outdoor vegetation fires?

☐ Yes. **STOP.** Tick DECLARATION box and Save this form. Complete a **Environmental risk review form** and submit to the College Ethics Committee using the de which will appear at the top of this form once saved.

☐ No. Go to 5

5. Does your study involve **humans** as the focus of research, or make use of data collected from human subjects?

☐ Yes. Go to 10

☐ No. Go to 6

6. Does your study involve a living vertebrate or cephalopod?

☐ Yes. Go to 7

☐ No. Tick DECLARATION box and Save this form. You can begin your project once your supervisor has reviewed this assessment.

7. Is your study interventional (i.e it involves capture, handling, and/or confinement ⓘ)?

☐ Yes. Go to 8

☐ No. **STOP.** Tick DECLARATION box and Save this form. Complete an **Animal vertebrate review form** and submit to the College Ethics Committee using the de which will appear at the top of this form once saved.

8. Is the intervention being carried out by Swansea University staff or students?

☐ Yes. Go to 9

☐ No. **STOP.** Tick DECLARATION box and Save this form. Complete an **Animal vertebrate review form** and submit to the College Ethics Committee using the de which will appear at the top of this form once saved.

9. Is the work being carried out in the field (UK or internationally) or at Swansea University campuses?

☐ Yes. **STOP.** Tick DECLARATION box and Save this form. Complete an **AWERB review form** and submit to the AWERB group using the dedicated link which will the top of this form once saved.

☐ No. **STOP.** Tick DECLARATION box and Save this form. Complete an **Animal vertebrate review form** and submit to the College Ethics Committee using the de which will appear at the top of this form once saved.

10. Does the proposed research involve any of the following?

You will find **Human Research Subjects Example Definitions** at: Ethics Resources

A. Vulnerable people, protected groups or participants unable to give informed consent. ⓘ ☐ Yes ☐ No

B. Sensitive topics or research material. ⓘ ☐ Yes ☐ No

C. Deception, misrepresentation or covert research. ⓘ ☐ Yes ☐ No

D. A risk of harm, distress or damage to anyone. ⓘ ☐ Yes ☐ No

E. Collection of **personal data** or **sensitive personal data** as defined in UK law (Data Protection Act; General Data Protection Regulation). ⓘ ☐ Yes ☐ No

F. Any other aspects that pose significant ethical concerns? ⓘ ☐ Yes ☐ No

G. Data collection from research participants without prior, recorded, informed consent? ⓘ ☐ Yes ☐ No

H. The sharing of data or confidential information beyond the initial consent given? ⓘ ☐ Yes ☐ No

I. A lack of anonymity for research participants? ⓘ ☐ Yes ☐ No

If Yes to **any** of the above, **STOP.** Tick DECLARATION box and Save this form. Complete a **Human Research Ethics review form** and submit to the College Ethics Co using the dedicated link which will appear at the top of this form once saved.

If No to **all** the above, Tick DECLARATION box and Save this form. You can begin your project once your supervisor has reviewed this assessment.

CONFLICTS OF INTEREST

Tick this box if there are any conflicts of interest to be declared. ⓘ ☐

Please email College Ethics Committee with details of conflicts: cosethics@swan.ac.uk. Please note, an approval number cannot be gi approval has been given by the College ethics committee and you should not start data collection until this has been given.

DECLARATION

I certify that the answers to the questions given above are true and accurate to the best of my knowledge and belief and I take full res for it. I also confirm that I have read the University's Policy Framework on Research Ethics & Governance and will abide by its ethical gu as well as the ethical principles underlying good practice appropriate to my discipline. ☑

Ethics Assessment for new project

Feedback:

Risk Assessment for Teaching, Administration and Research Activities

Swansea University; College of Science

Name Megan Watts **Signature** [redacted] **date** 06/05/2020

Supervisor* Dr Will Allen **Signature** [redacted] **date** 06/05/2020

Activity title Comparing the rate of weapon and ornament diversification **Base location (room no.)** ....

(* the supervisor for all HEFCW funded academic and non-academic staff is the HOC)

University Activity Serial # (enter Employee No. or STUREC No ....
Start date of activity (cannot predate signature dates) 06/05/2020
End date of activity (or 'on going') On going

Level of worker (delete as applicable) ....

~~UG~~, [✓ PG], ~~research assistant~~, ~~technician~~, ~~administration~~, ~~academic staff~~, ~~other (state)~~

Approval obtained for Gene Manipulation Safety Assessment by SU ? ~~Yes~~/not applicable
Licence(s) obtained under "Animals (Scientific Procedures) Act (1986)" ? ~~Yes~~/not applicable
Approval obtained for use of radioisotopes by COS ? ~~Yes~~/not applicable

Record of specialist training undertaken

Course	date

Summary of protocols used; protocol sheets to be appended plus COSHH details for chemicals of category A or B with high or medium exposure

Protocol Details						Protocol Details					
#	Assessment					#	Assessment				
	1st date	Frequency of re-assessment	Hazard category	Secondary containment level	Exposure potential		1st date	Frequency of re- assessment	Hazard category	Secondary containment level	Exposure potential
1						11					
2						12					
3						13					
4						14					
5						15					
6						16					
7						17					
8						18					
9						19					
10						20					

See notes in handbook for help in filling in form **(Continue on another sheet if necessary)**

Bioscience and Geography Protocol Risk Assessment Form

(Expand or contract fields, or append additional sheets as required; insert NA if not applicable)

Protocol #	**Title:** Comparing the rate of weapon and ornament diversification.
Associated Protocols #..........................	**Description:** Using published literature and museum collections to test the hypothesis that traits under selection via female choice should evolve faster than those under selection via male-male competition.

Location:

circle which Bioscience and Geography Local Rules apply –

Boat **Field** **Genetic-Manipulation** **Laboratory** [✓ **Office/Facility**] **Radioisotope**

Identify here risks and control measures for work in this environment, additional to Local Rules

Office space is comfortable, regular breaks will be taken, correct eyewear will be worn.

Chemicals	Quantity	Hazards	Category (A,B,C,D)*	Exp. Score

Hazard Category (known or potential)

- **A** (e.g. carcinogen/teratogen/mutagen)
- **B** (e.g. v.toxic/toxic/explosive/pyrophoric)
- **C** (e.g. harmful/irritant/corrosive/high flammable/oxidising)
- **D** (e.g. non classified)

Exposure Potential Circle the **highest Exposure Score** above. Use this to calculate the exposure potential for the entire protocol (see handbook). Indicate this value below.

Low **Medium** **High**

Primary containment (of product) sealed flask/bottle/glass/plastic/other (state) :-

Storage conditions and maximum duration :-

Secondary containment (of protocol) open bench/fume hood/special (state) :-

Disposal e.g. autoclaving of biohazard, SU chemical disposal

Identify other control measures (circle or delete) - latex/nitrile/heavy gloves; screens; full face mask; dust mask; protective shoes; spillage tray; ear-defenders; other (state)

Justification and controls for any work outside normal hours

Emergency procedures (e.g. spillage clearance; communication methods)

~~Supervision/~~training for worker (circle)

[✓ None required] Already trained Training required Supervised always

Declaration I declare that I have assessed the hazards and risks associated with my work and will take appropriate measures to decrease these risks, as far as possible eliminating them, and will monitor the effectiveness of these risk control measures.

Name & signature of worker ......[redacted]..

Name & counter-signature of supervisor...........[redacted].............. *Date*...06/05/2020...

Date of first reassessment Frequency of reassessments

Guidance for Completion of Bioscience and Geography Protocol Risk Assessment Form

Note – you are strongly advised to complete electronic versions of this form, enabling you to readily expand and contract sections as required to ensure clarity and adequate documentation. Do **not** delete any sections! Instead, mark inappropriate sections with NA (not applicable) and contract the section to save space on the final printed form.

Protocol - any self-contained procedure. This could be any activities undertaken, be they lab-work, use of equipment, fieldwork or office work. Your complete research/teaching/administration **activity** (e.g. undergraduate project, PhD study, research grant, other) is therefore made up from separate **protocols**. If the protocol is mainly of low hazard, but with one or more hazardous components, consider making the manipulation of the latter a separate protocol and tie them together by completing the "*Associated Protocol*" box. This is because the entire protocol must be conducted under conditions required for the handling of the most hazardous component.

Title/Description - give sufficient detail to make it obvious what the protocol involves.

Location – identify which local rules apply. More than one rule may apply. Then add any additional risks and control measures peculiar to this protocol (e.g. site-specific fieldwork information; use of autoclaves, sonicators; mechanical, electrical hazards). You may also wish to stress any particularly important risks and controls even if indicated in local rules.

Chemicals etc. - give name, maximum quantity used, list hazards, hazard category (see Table 1) and calculate the **Exposure Score** (see Table 2) for **every** chemical used. Expand the area in the table as required.

Exposure Potential (see Table 3) - complete this section for the chemical which has the **highest** exposure score in your chemical list as this defines the highest risk factor.

Primary containment/Storage - detail how and where, and for how long, the resultant product from the protocol will be stored. The product must be labelled with the date of synthesis, and disposed of (see below) before the maximum duration time has elapsed.

Secondary containment - detail where the protocol will be performed (refer to Table 4).

Disposal - detail how you will dispose of surplus reagents and the product of the protocol. Final disposal must be undertaken within the period noted in the 'maximum duration' under 'Storage' (above).

Identify other control measures – typically these refer to special protective clothing etc.

Justification and controls for any work outside normal hours – out of hours working is only allowed under special conditions (e.g. 24h sampling, sampling related to tides etc.); convenience is not an acceptable reason.

Emergency procedures - detail how spillages etc. would be handled, including clearance of the laboratory etc. as required. For field work indicate emergency communication and first-aid coverage.

Supervision/training - detail here what special supervision and training is required by the worker named at the bottom of the form. Note that all undergraduates are always considered as research incompetent. First-year PhD students and MSc students are not to be used to supervise the activities of others.

Declaration - both the worker and the supervisor must sign this on the date entered here.

Reassessment - the first reassessment must be undertaken as soon as possible after the first time the protocol has been undertaken in order to identify any unforeseen hazards. After this first reassessment, the protocol should be reassessed every 6-12m, depending on the nature of the chemicals, to take account of changing knowledge concerning the hazardous nature of chemicals. The protocol must be reassessed immediately if new knowledge on the chemical hazards becomes available.

NOTE - standard protocols can be produced for each environment BUT each worker must have their own personalised version, signed by them and their supervisor, and dated. These completed personalised protocols must then be appended to the SU risk assessment form for the Teaching/Research activity belonging to the individual.

COSHH Assessment - modified from "COSHH in Laboratories" published by the Royal Society of Chemistry, July 1989

Hazards, Risks and Containment - Definition of terms

Hazard	potential for doing harm, *e.g.* toxic, flammable, carcinogenic *etc*
Exposure potential	the risk to the user depends very much on the exposure, which depends on the physical properties of the material, the quantity used and for how long.

Risk = "Hazard" x "Exposure Potential"

The risk is decreased to a safe level by:

a) Containment
b) Personal Protection
c) Good Laboratory Practice (GLP)

Levels of containment

The containment required for a given activity is of two basic kinds: the primary (or intrinsic) containment provided by the apparatus or equipment in which the substances are handled and the additional (or secondary) containment needed to ensure appropriate control of exposure.

HAZARD CATEGORY

TABLE 1- General Guidelines for determining hazard categories

A	EXTREME HAZARD	Substances of known or suspected exceptional toxicity (e.g. carcinogen, teratogen, potential mutagen)
B	HIGH HAZARD	All substances whose toxicity exceeds that of the medium hazard category, except for those known or believed to be so highly toxic as to merit special precautions (i.e. those in the "extreme" category)
C	MEDIUM HAZARD	Substances meeting criteria for CPL* classification as "Harmful" or 'Irritant'
D	LOW HAZARD	Substances not matching criteria for CPL* classification as "Harmful" or "Irritant"

CPL = the Classification, Packaging and Labelling Regulations 1984.

NOTE:

1. The toxicity considered should be that of the substance or mixture handled, including any impurities.
2. Substances may have other properties (*e.g.* flammability) which may call for additional precautions.
3. The above general guidance may need to be supplemented by developing additional criteria with the help of expert toxicological advice. (Additional criteria may be developed using, for example, data given in HSE Guidance Notes such as EH40).
4. Time factors, such as frequency and duration of activity should also be considered. Short duration tasks, involving a few seconds exposure at infrequent intervals, should not affect the initial estimate, whereas continuous operations on a daily basis would probably raise the estimate to the next highest category.

EXPOSURE SCORE

TABLE 2 - exposure score to be calculated for all chemicals used in a protocol

EXPOSURE SCORE				
Calculation Value		**1**	**2**	**3**
(i)	Quantity	<1g	1-100g	>100g
(ii)	Properties	Dense solid Non- volatile liquid No skin absorption	Dusty solids Lyophilised solids Volatile liquids (b.p.>80ºC)	Gases, Aerosols Highly volatile liquids (b.p.<80º C) Solutions promoting skin absorption
(iii)	Pressure	Normal	Low/Vacuum	>1 atmosphere
(iv)	Temperature	Room temperature	25ºC - 100ºC	>100ºC

Exposure Score calculation = (i) x (ii) x (iii) x (iv)

The Exposure Potential

TABLE 3 - Rough calculation of exposure potential

	EXPOSURE SCORE (FROM TABLE 2)		
Total score	**<10**	**10-54**	**>54**
Exposure Potential	**L** (low)	**M** (medium)	**H** (high)

Secondary containment level calculation

Table 4 - use to determine secondary containment

SECONDARY CONTAINMENT LEVEL					
Hazard Category		**A**	**B**	**C**	**D**
Exposure potential (from table 3)	**H**	SA	SA	FH	FH
	M	SA	FH	FH	OB
	L	FH	FH	OB	OB

OB = **O**pen **B**ench; **FH** = **F**ume **H**ood; **SA** = **S**pecial **A**ttention (see supervisor)

Introduction

The foundations of the modern sexual selection theory were first proposed in “The Origin of Species” *(Darwin, 1859)* and expanded on in “The Descent of Man, and Selection in Relation to Sex” *(Darwin, 1871)*. The theory tried to explain how traits that did not appear to increase survival but increased fitness of an individual evolved without being favoured by natural selection *(Shuker & Kvarnemo, 2021)*. In this work Darwin explains the theory of sexual selection to account for organismal traits such as the peacock’s tail that appeared to hinder survival and so could not easily be explained by natural selection *(Darwin, 1871).* Darwin identified two mechanisms of sexual selection that are still recognised today, male-male competition (intrasexual selection) and female choice (intersexual selection). Intrasexual selection is the result of interaction between a singular sex of one species, this refers to competition between members of the same sex *(Darwin, 1871)*. Intersexual selection is the result of interaction between the sexes of one species, this is characterised by choice of mates from the opposite sex *(Moore, 1990)*.

Intrasexual selection can result in the development of weapons in one sex, typically males, to compete with other males for mating rights. Males with ‘better’ weapons are more likely to win encounters with rival males, and so secure more mating opportunities, passing their genes for high quality weapons to the next generation. As well as improving combat ability weapons can function as signals to other males fighting ability of a male *(Emlen, 2008b)*. Weapons are often diverse in size and shape and are found in a range of taxa *(Rico-Guevara & Hurme, 2018)*. Some examples of weapons are stag beetle horns *(Kijimoto et al., 2013)*, and fiddler crab claws *(Callander et al., 2013)*. The relative size of weaponry generally positively correlates with individual mating success *(Emlen, 2008a)*. Larger weaponry is not always possible, natural selection costs can constrain male weapons *(Bro-Jorgensen, 2007).* Males with more elaborate and large weapons can lose functionality of the weapon and therefore would perform poorly against predators and males with more functional weapons *(Bro-Jorgensen, 2007)*.

Intersexual selection can lead to the development of ornaments in males due to female mate choice *(West-Eberhard, 1983)*. In order to impress females, males of some species have developed ‘flashy’ ornamental traits to appeal *(Iwasa et al., 1991)*. Female preferences for ornamented males result in non-random mating, with males possessing preferred ornaments having increased reproductive success, and so passing copies of the ornament gene(s) to the next generation. Some examples of ornaments are bright colouration *(Badyaev et al., 2001)*, long tails *(Matyjasiak el al., 2001)* and large or intricate horns *(Emlen, 2001)*. These signals can be reliable indicators of male quality *(Searcy & Nowicki, 2005)*. In order to provide a reliable signal to females there must be a limit on the size and diversity of male ornamentation. The limit is outlined by the cost of adopting ornaments to the males' fitness. Males can be negatively affected by large or asymmetric ornaments affecting their maneuverability *(Moller, 1991).* Lower maneuverability makes males more susceptible to predator attack and therefore lowering their fitness. For example, male swordtail fishes *(Xiphophorus)* with swords are found to be attacked more frequently by predators than their swordless counterparts *(Hernandez-Jimenez & Rios-Cardenas, 2012)*.

Although weapons and ornaments have different functions, these two types of sexually selected structure are best thought of as operating on a continuum where weapons can function as ornaments *(Berglund et al., 1996; McCullough et al., 2016)*. The dual functionality of traits may arise from females choosing males with weapon traits that associate with male quality, or males responding to signal traits that initially evolved through female choice *(Berglund et al., 1996)*. An example of a weapon which is also an ornament is fiddler crabs *(Uca)* which have a single enlarged claw which is used for sparring with males and signalling to females *(Allen & Levington, 2007)*. In this example it is thought that male-male competition is driving weapon diversification, not female choice as weapons are first and foremost fighting structures *(McCullough et al., 2016)*. For this study I tried to only weapons use purely for competition will be compared to eliminate the risk of using a weapon that is also an ornament.

The overall selection pressure leading to the evolution of weapons and ornaments is the same – competition for mating opportunities. However, the history and rate of weapon and ornament evolution is predicted to be different *(McCullough et al. 2016).* This is because weapons are only under selection in males, whereas ornament traits and preferences for particular ornaments coevolve in males and females. Under the Fisherian model of sexual selection *(Fisher, 1915; Fisher, 1930; Lande, 1981),* in a population where males genetically vary in ornamental traits, when females have (genetic) preferences for more elaborate male ornaments the males with the most elaborate traits will have the highest reproductive success *(Kuijper et al., 2012)*. This leaves relatively more copies of both the elaborate ornament and elaborate preference genes in the next generation. A genetic correlation therefore develops between the female preference for a male ornament trait and the ornament trait *(Mead & Arnold, 2004)*. The selection on ornamentation creates positive feedback between the genes that influence the form of ornaments and those that influence preferences *(Fisher, 1930)*. The 'Fisher process' then escalates the rate of evolution of female mate preferences and male ornaments *(Andersson, 1994).* The Fisher process allows the female preference trait to evolve relatively fast as females with preferences for the most exaggerated traits will produce more attractive male offspring, and female offspring with relatively extreme preferences. This 'runaway' process can then repeat in the next generation and continue to produce ever more elaborate ornaments until natural selection acts against more extreme ornament forms. Evidence for Fisherian runaway selection is relatively little and has mainly been done in theoretical experiments rather than on real world data *(Pomiankowski et al., 1991; Pomiankowski & Iwasa, 1998; Hall et al., 2007; Bailey & Moore, 2012)*. Physical evidence for Fisherian processes have been limited to single taxa and traits such as male song pulse in *Laupala* crickets *(Xu & Shaw, 2019)* and bird plumage *(Price, 1998; Kose & Moller, 1999; Cooney et al., 2019)*.

Weapons may also be expected to evolve slower than ornaments because sexual selection on male weapons only occurs in the male line, even though females may still carry genes that influence weapon form *(Lukasiewicz et al., 2020)*. This is expected to effectively reduce the strength of selection because male offspring will inherit traits of females with ‘hidden’ sub-optimal weapon genes, which would slow the rate of trait evolution *(Jennions & Petrie, 2000)*. Thirdly, weapons may evolve slower than ornaments because they might generally have a smaller trait space than ornaments due to the relatively unconstrained nature of some ornament traits compared to weapon traits. For example a visual signal can vary in size, colour, brightness and motion, and might also be paired with high-dimensional acoustic, behavioural, or other sensory components *(Higham & Hebets, 2013)* with the form of the signal relatively unconstrained by function *(Hebets & Papaj, 2005)*. In contrast, because the performance of weapon traits used in male-male combat is tightly linked to form, =a smaller trait space could decrease the rate of weapon diversification *(Berglund et al., 2013)*.

Comparative studies that have compared the rates of evolution across different classes of sexually and non-sexually selected traits have shown that sexually selected traits are subject to accelerated rates of evolution *(Simmons & Fitzpatrick, 2016)*. As sexual selection is a driver of trait diversification both weapon and ornaments diversification rates are expected to be higher than non-sexually selected traits *(Seddon et al., 2013)*. In African mormyrid fishes it was found that sexually selected signalling evolved rapidly when compared to naturally selected traits such as morphology, size and trophic ecology *(Arnegard et al., 2010)*. The difference in rates was attributed to expansion of trait space allowing new opportunities for communication *(Arnegard et al., 2010)*. In this thesis I will extend these investigations to examination variation in the rate of evolution between sexually selected traits, testing the hypothesis that ornamental traits evolve more quickly than weapon traits using weapon and ornament trait data from a range of taxa and use a recently developed phylogenetic comparative method ratebytree *(Revell et al., 2018)* to compare the rates of evolution of weapons and ornaments.

The *ratebytree* function estimates the rate of evolution using common rate and multiple rate models *(Revell et al., 2018)*. The algorithm is able to incorporate three evolutionary models into the analysis. These are Brownian motion (BM), Ornstein-Uhlenbeck process (OU), and early burst model (EB). BM is the default model and is an example of a “random walk” model as the trait value can change in proportion to units of time *(Kac, 1947)*. OU and EB can be selected for within the *ratebytree* function. OU is a modified version of random walk adding the ‘rubber band effect’, where the change is without limit, but traits tend to gravitate to an optimum value *(Hansen, 1997)*. EB assumes a ‘burst’ in evolution rate, where traits are developed quickly, then the rate slows through time after the ‘burst’ event *(Harmon et al., 2010)*. As all traits have to be modelled under the same regime in the *ratebytree* analysis, to ensure that the most appropriate model is used I will fit these three models to each individual trait dataset to establish which of the three overall best models the evolution of sexually selected traits.

This analysis follows on from a previous unpublished Masters thesis (Hutton 2019). This found some support for the hypothesis that ornaments evolve faster than weapons, but interpretation of results was difficult because evolutionary rates are expected to increase for lineages with shorter generation times, and the ornamental trait datasets may have had shorter generation times that the weapon trait datasets. Additionally, because of a strong relationship between lineage age and the rate of trait evolution was observed, with older lineages showing reduced evolutionary rates (*Harmon et al., 2021*), different lineage ages of weapons and ornaments may have influenced the overall estimate of the rate of evolution of weapons and ornaments. The design of this study seeks to minimise the effect these factors might have on results by selecting pairs of ornament and weapon trait datasets from closely related taxa, which should have more similar evolutionary ages and generation times. Closely related taxa often experience similar selection pressures related to the rate of trait evolution, such as rate of reproduction and lifespan *(Ord & Summers, 2015)*.

This thesis is exploring a key prediction from sexual selection theory in a novel way. The widespread role of Fisher runaway processes in the evolution of ornamental traits does not yet have supporting evidence across diverse taxa and traits. If the hypothesis that ornaments evolve faster than weapons is supported this will be the first macroevolutionary scale results to potentially give support in favour of widespread Fisherian processes. The comparison of evolutionary rates of weapons and ornaments in similar taxa using a paired dataset method is a novel approach which has not previously been explored in this way.

Methods

The overall approach to data collection was to build on the previous dataset compiled by Hutton (2019) to establish a ‘matched pairs’ design of weapon and ornament traits. Pairs of weapon and ornament traits comprised taxa more closely related to each other than any of the other taxa in the study. This attempts to control for the variation in the rate of evolution between taxa due to, for example, varying generation times and lineage ages.

Literature Search

The foundation of the dataset used in this study were the nine ornament and five weapon traits gathered by Hutton (2019) from the primary literature and museum collections. These were double-checked for meeting inclusion criteria. These were:

1.) They measure a trait thought to be a relatively ‘pure’ weapon or ornament (i.e. a weapon not also used in female choice, or an ornament not used in male-male competition). In cases where there is some evidence that weapons also function as ornaments (e.g. bovid horns *Bro-Jorgensen 2007; Barmann et al., 2013; Lupold et al., 2015*), the trait must have strong evidence that evolved diversity has principally been driven by its functionally used as either a weapon or an ornament.

2.) The phenotype was measured on an ordinal or fully continuous scale on one or more dimensions, or on multiple binary traits.

3.) A time calibrated molecular phylogeny for at least ten of the species in the dataset was available.

All the datasets included in Hutton's (2019) thesis met criteria.
There were nine ornament datasets used from Hutton, 2019 Masters thesis. They were stalk-eyed-fly eyespan, dragonfly posterior wing pigmentation, birds-of-paradise plumage score, cuckoo plumage score, old world orioles plumage score, true finches plumage score, gallinaceous birds plumage score, gliding lizard dewlap area and primate ornament score. The only ornament datasets not used was the fairy wren dataset as it was the smallest datasets of all the bird ornament scores and there were already four other bird datasets being included *(Dale et al., 2015; n=27)*.

Of the Hutton, 2019 weapon datasets all five were used which were artiodactyl tusk length, bovid horn length, stag beetle horn length and gallinaceous birds spur length. None were excluded as all the datasets fit the inclusion criteria and were across diverse taxa.

I then searched for additional datasets that met inclusion criteria. I based this search on two review papers. The Rico-Guevara and Hurme (2018) review “Intrasexually selected weapons” was used to discover taxa with intrasexually selected weapons, and to find ornaments the Wiens and Tuschoff, 2020 review “Songs versus colours versus horns: what explains the diversity of sexually selected traits?” was used. These reviews provide tables of examples of traits identified as weapons and ornaments across diverse taxonomic groups. I went through the tables systematically aiming to identify additional comparative datasets and check they met inclusion criteria. Datasets were downloaded from journal supplementary materials, datadryad.org, figshare.com, and datasetsearch.research.google.com.

Pairing Datasets

From the set of potential traits, I began the process of pairing weapon and ornament traits. The goal was to create pairs of traits from taxa more closely related to each other than any of the other taxa included in the study. To establish this, I consulted online taxonomies and phylogenies (e.g. http://www.onezoom.org/, http://tolweb.org/) and used http://timetree.org/ to check estimated divergence times for pairs of taxa.

In several instances it was straightforward to pair a weapon and ornament trait, for example pairing the primate weapon and ornament datasets. For other potential datasets the potential matched pair was less closely related or there was no closely related pair among the available datasets. In this instance I returned to check the reviews to identify potential pairings. Once a taxonomic group was identified as a potential suitable pair for an available dataset an extensive literature search using Google Scholar was undertaken methodically searching for suitable comparative trait data on the taxonomic group or a subgroup. This method is how the ibis

(Pelecaniformes) weapon, gallinaceous bird and agamid lizard ornament datasets were identified.

When this process did not locate comparative data to form a pair with one of the datasets already established, I explored whether creating a new comparative dataset from existing literature (e.g. multiple single-species studies) was feasible, such as the habronattus jumping spider and bat ornament datasets This method will be further explained in the next section. When this was not feasible, remaining unpaired traits were not used in the analysis. These included fiddler crab weapons, earwig weapons and katydid ornaments.

For some datasets there were multiple potential datasets that could be paired with it (i.e. data from a group more closely related to the pair than all other datasets). In this instance, to maximise the data analysed and to enable the consistency of the rate of trait evolution and the effect of dataset choice on the rate of weapon and ornament evolution to be investigated, all potential pairs were included. For example, the bat ornament dataset had three weapon datasets paired with it (carnivore canine length, artiodactyl tusk length and bovid horn length). Analyses were repeated for each of the three pairs to establish whether interpretation of results depended on which dataset was included.

Formation of New Datasets

Two new ornament datasets were created to match weapon datasets. These were the bat song dataset to match the carnivore canine height dataset, and the habronattus jumping spider colouration dataset to match the harvestman fourth coxa weapon dataset.

The bat song dataset was created from the Smotherman et al., 2016 paper "The origins and diversity of bat songs" using information extracted from text about bat song structure. Bats are social animals and singing is used in a similar way to bird songs, generally the most common use is territoriality and mating *(Smotherman et al., 2016)*. On the basis of information in the paper a binary scoring system was created with categories identified from the paper. These categories were song, call, complex motifs, basic motif, series, different syllable, simple syllable, and same variable syllable. If the species used any of these in their call structure it would be given a one, if not a zero. Multidimensional scaling (MDS) was then applied to the binary trait matrix to construct a call complexity dimension on which each species was scored *(Kruskall, 1997)*.

The habronattus jumping spider dataset was created to match the harvestman as a known ornamented arachnid group *(Taylor & McGraw, 2013)*. The species selected to form the dataset were based on the species included in a recent comprehensive phylogeny of the jumping spiders *(Leduc-Robert & Maddison, 2018)*. Some species of jumping spider use complex visual signals to attract mates *(Elias et al., 2005)*. Colour and pattern on the spiders' pedipalp, face, first, second and third leg are all recognised as potentially being components of ornamentation in the group *(Taylor & McGraw, 2013)*. I scored these traits across the species included in the phylogeny. An image of each species was examined and each of the five body parts was given a score between zero to five depending on how extreme the ornamentation was:
0: No ornamentation; monochromatic and lack of other ornamental features.
1: More than one colour with no bright colours.
2: More than two colours with no bright colours.
3: More than two colours with some bright colours.
4: More than two colours with mostly bright colours.
5: Extreme colouration and patterns.

Figure 1 – a. Habronattus conjunctus was given a high mds score for ornamentation (mds = 4.045) which means the level of ornamentation is low. Apart from the face which received a score of 2 as it had more than two colours on its face all the other features were marked 0. Image source Kaldari, 2011.
b. Habronattus chamela was given an average mds score for ornamentation (mds = 0.053) as the spider had ornamentation on its face and some contrasting colours on the rest of its body but was overall rated averagely ornamented. Image source Maddison, W 2015.
c.Habronattus americanus was rated highly ornamented (mds = -4.210) due to extreme colouration and contrast across multiple body parts related to sexual signaling. Image source Hart, S Hart, 2013.

Images were found on Google Images and then confirmed as the correct species using bugguide.net. Traits were scored by a single investigator. MDS was applied on the matrix of trait scores to derive an overall ornamentation score for each species that quantified how elaborate the overall ornamentation was *(Kruskal, 1977)*.

In total 22 weapon and ornament datasets were identified to form seven matched pairs (see table 1). Of these 15 were sourced from Hutton, 2019, five were identified from reviews and Google Scholar and two were formed for the thesis.

Table 1 *- Overview of all 22 datasets used in analysis. Weapon and ornament datasets are paired with similar taxa with ID being a key to paired datasets. Taxa is the taxonomic group that the trait dataset comes from. N is the number of species in the trait dataset that is used in analysis. The data source and phylogeny source are the original source papers for the data.*

ID	***Weapons***					***Ornaments***				
	Taxa	***N***	***Trait***	***Data source***	***Phylogeny source***	***Taxa***	***N***	***Trait***	***Data source***	***Phylogeny source***
1	Carnivores *(Carnivora)*	43	Canine length	Gittleman, 1997	Upham et al., 2019	Bats *(Chiroptera)*	23	Song features	Smotherman et al., 2016	Teeling et al., 2005
	Artiodactyl *(Artiodactyla)*	62	Tusk length	Cabrera & Stankowich, 2018	Upham et al., 2019					
	Bovid *(Bovidae)*	116	Horn length	Bro-Jorgensen 2007; Barmann et al., 2013; Lupold et al., 2015	Upham et al., 2019					
2	Stag beetles	26	Horn length	Hutton, 2019	Kim & Farrell, 2015	Stalk-eyed-flies *(Diopsidae)*	31	Eye span	Lupold et al., 2015	Lupold et al., 2015
	Leaf-footed beetle *(Coredae)*	17	Hind leg shape	Emberts et al., 2021	Emberts et al., 2021	Dragonflies *(Odonata)*	30	Posterior wing pigmentation	Santos & Machado, 2016	Carle et al., 2015
3	Ibis *(Pelicaniformes)*	10	Beak length	Babbit & Frederick, 2007	Jetz et al., 2012	Birds-of-paradise *(Paradisaeidae)*	36	Plumage score	Dale et al., 2015	Jetz et al., 2012
						Cuckoos *(Cuculiformes)*	128	Plumage score	Hasegawa & Arai, 2018	Jetz et al., 2012
						Old world orioles *(Oriolidae)*	35	Plumage score	Dale et al., 2015	Jetz et al., 2012
						True finches *(Fringillidae)*	190	Plumage score	Dale et al., 2015	Jetz et al., 2012
4	Harvestman *(Opiliones)*	12	Fourth coxa length	Buzatto et al., 2014	Benavides et al., 2020	Jumping spiders *(Habronattus)*	32	Body ornamentation	This study	Leduc-Robert & Maddison, 2018
5	Gallinaceous birds *(Galliformes)*	103	Spur length	Sullivan, 1993	Jetz et al., 2012	Gallinaceous birds *(Galliformes)*	62	Plumage score	Bitton, 2017	Jetz et al., 2012
6	Anolis lizards *(Anolis)*	27	Bite force	De Meyer et al., 2019	Tonini et al., 2016	Gliding lizards *(Draco)*	10	Dewlap area	Klomp et al., 2016	Tonini et al., 2016
						Agamid lizard *(Agamidae)*	42	Ceratiobranchial length	Ord et al., 2015	Tonini et al., 2016

7	Primates *(Primates)*	100	Canine length	Lupold et al., 2015 & Lupold et al., 2019	Upham et al., 2019	Primates *(Primates)*	91	Ornament score	Lupold et al., 2019	Upham et al., 2019

Phylogenies

The comparative analyses of rates of trait evolution require dated phylogenies. For the datasets taken from Hutton (2019) these were already available. For the other traits, with the exception of the habronattus jumping spider dataset, where species trait data search was based on the species included in habronattus phylogeny of Leduc-Robert & Maddison (2018), the phylogenies for the new trait datasets were identified after collecting the trait dataset.

For the remaining datasets (bats, leaf-footed bugs, ibis, harvestman, agamid lizards and dragonfly) the phylogenies searched for synchronously during the pairing process using Google Scholar with the search term “phylogeny” and the name of the taxa. The taxonomic information used in the phylogeny search would start as specific as possible, starting with the specific taxonomic group (e.g. *Coredidae*). If this was not successful, then higher taxonomic levels were searched for (e.g. *Hemiptera*). If an appropriate time-calibrated molecular phylogeny could not be identified after searching at higher taxonomic levels, then the trait dataset was not used. This process removed some trait datasets from the study such as fiddler crabs as no suitable phylogeny was available. After removing a trait dataset due to lack of phylogeny another lead was followed to find an appropriate pair.

I ensured the branch length of all phylogenies were given in units of millions of years.

Data preparation

In order to use the datasets and phylogenies for analysis I worked through the datasets and phylogenies to ensure that all the species names were in the format “Genus_species” and that species names conformed to those in the latest taxonomies. The R package “taxize” was used for this to resolve any names containing typos or outdated species names *(Chamberlain & Szocs, 2013)*. The taxize package searches through the datasets and phylogenies and flags any names that do not match the most up to date species names from over many websites *(Chamberlain & Szocs, 2013)*. The names flagged were then manually changed in the datasets or phylogenies. The trait datasets were examined and if species were missing data on traits of interest the species were removed from the dataset.

A file naming system was put into place to make reading the datasets into R straightforward and avoid errors. Each pair of datasets were assigned a number to match, then the dataset was marked either “w” for weapon or “o” for ornament and then the species group at the end. For example, the bat trait dataset was labelled 1_o_bat with the same phylogeny name.

Once the datasets only contained species with complete data the trees were matched with the data in order to ascertain the species in the datasets that were not in the phylogenies and vice versa. Further typos and mismatches between names were corrected.

Once the datasets and phylogenies had as many matching species as possible the incomplete species were removed from either the tree or the dataset. This left the datasets and trees with the same list of species.

Comparing the evolutionary rates of weapons and ornaments

The analysis of the rate of trait evolution for weapons and ornaments was undertaken in R. The packages used were “phytools”, “nlme”, “geiger”, and “caper” *(Revell, 2011; Karlsson et al., 2015; Pennell et al., 2014; Orme, 2018)*. The phylogenetic trees and trait datasets were initially read into R. The trait data consisted of the measures of weapons or ornaments and in cases where the size of species might influence the size of the trait, body size data was also imported.

Body size was expected to be correlated with several of the trait datasets included in the analysis. While body size can be under sexual selection, for example for increased fighting ability *(Price, 1984),* it is also under many other ecological and physiological selection pressures. To isolate the influence of sexual selection on trait evolution I wanted to analyse body-size independent trait evolution so I tested whether there was a relationship between the sexual trait and body size using phylogenetic generalised least squares (PGLS*, Grafen 1989; see table 2*). If the relationship between body size and evolution was significant the residuals of the regression were used for analysis.

I ran PGLS in the R “phytools” *(Revell, 2011)* package estimating Pagel’s lambda, which scales branch lengths of the phylogenetic tree to model trait relationships with the appropriate degree of phylogenetic control.

As most of the traits were measured on different scales to establish an equivalence of evolutionary rates in trait space they required standardisation *(Overington et al., 2009).* To standardise the traits across datasets z-scores were taken. This means that all the traits were comparable and removes bias of species measured on longer scales or with larger trait space having higher evolutionary rates *(Rolhausen et al., 2018)*.

The rate of diversification was measured for single traits under BM, OU and EB models (see table 3). The R package “geiger” *(Karlsson et al., 2015)*, is used with the function “fitCotinuous()”. Each trait was analysed individually to fit each trait to the model that most accurately describes the evolutionary scenario using the Akaike information criteria (AIC; *Jhwueng et al., 2014*). A single rate for diversification (σ^2)

for each trait was also output from the fitContinuous function, which was used to identify the slowest evolving ornament traits to match against the fastest evolving ornament traits.

The function *ratebytree (Revell et al., 2018)* was used to compare the rates of evolution of weapons and ornaments. The function works by comparing the Brownian rate of evolution between the trees which is the common rate model. Then the function compares the rate in a multiple rate model where the trees can have different rates *(Revell et al., 2018)*. To investigate whether the result was consistent the function ran in iterations with all 96 combinations of the matching weapon and ornament datasets. In the results section I present the results of the analysis that includes the most conservative weapon-ornament pairs for pairs where there was more than one weapon or ornament dataset (Table 1) – i.e. the pair with the slowest evolving ornament and the fastest evolving weapon. The results for other combinations are presented in the appendix.

The *ratebytree* function *(Revell et al., 2018)* compares evolutionary rates under one of three evolutionary models: BM (*Felsenstein, 1985*), OU (*Lande, 1976*), and EB (*Harmon et al., 2003*). The same evolutionary model is applied to all datasets in the analysis. As different datasets might be best modelled with different evolutionary models, I had to choose which of these three models overall was the best choice. In order to identify which of these choices were most appropriate for the datasets overall, the three models were fitted to each individual dataset and model support was assessed using AIC scores (Burnham & Anderson 2004). The model used in the main *ratebytree* analysis was the model which fitted the most individual datasets, with results under other models presented to assess whether this choice influenced conclusions.

The *ratebytree* function takes as input the set of phylogenetic trees and a list of trait vectors for the continuous traits. The function fits the evolutionary model (BM/OU/EB) to a.) all traits jointly – the common rate model and b.) the weapon and ornament traits separately – the multi-rate model *(Revell et al., 2018)*. It then uses a likelihood-ratio test to compare support for the common and multi-rate models *(Revell el al., 2018)*, testing whether weapons and ornaments in general evolve at different rates.

Plotting the traits on the phylogenies

To visualise the trait data in conjunction with the phylogenies the “contMap()” function in the “phytools” package *(Revell, 2011)* was used to plot the phylogenies with an estimate of trait evolution represented as branch colour. The function plots the traits on a continuous scale and shows that on the phylogeny with a heatmap. The colours range from blue to red, blue being less extreme traits and red being more extreme.

To show the difference in rates for weapons and ornaments violin plots were used. The R package “ggplot2” *(Wickham, 2011)* was used to plot these.

Results

The analysis is reported in three stages, first I examine whether select traits needed to be body-size corrected. I then investigate the fit of different evolutionary models to each trait individually and the rate of individual trait evolution.

The species found with a link between body size and trait size were carnivore canine length, artiodactyl tusk length, bovid horn length, anolis lizard bite force, primate canine length and stalk-eyed-fly eye span (Table 2). For these traits the residuals of the PGLS regression were analysed in the single-trait rate and *ratebytree* analyses.

Table 2 - Phylogenetic generalised least squares model results of the relationship between body size and trait size. Only traits that plausibly had a direct relationship with body size were analysed. The p-values that are highlighted with an asterisk are significant at $p<0.05$.

Taxa	Number of species	PGLS				
		Pagel’s λ	Standard error	t-value	p-value	Slope
Carnivore canine length	43	0.035	0.016	20.097	0.000*	0.320
Artiodactyl tusk length	62	0.988	0.162	-2.436	0.018*	-0.394
Bovid horn length	116	0.946	0.046	13.230	0.000*	0.615
Ibis beak length	10	1.000	0.203	1.557	0.158	0.316
Harvestman fourth coxa length	12	0.000	0.146	0.522	0.613	0.076
Gallinaceous bird spur length	103	0.991	0.315	1.761	0.081	0.554
Anolis lizard bite force	27	1.000	0.214	11.665	0.000*	2.500
Primate canine height	100	0.935	0.032	9.992	0.000*	0.318
Stalk-eyed-flies eye span	31	0.953	0.269	6.153	0.000*	1.658
Gliding lizard dewlap area	10	0.00	1.436	1.184	0.302	1.699
Agamid lizard ceratiobranchial length	42	0.394	0.408	-0.359	0.722	-0.176

The single trait analysis fitted three evolutionary models to the datasets (table 3). Of the three models OU was favoured for 14/23 datasets, eight datasets were favoured by the BM and none were favoured by the EB. Under the BM model the slowest evolving weapon trait was the harvestman ($\sigma^2 = 0.017$) and fastest evolving weapon trait was the bovid ($\sigma^2 = 0.124$), with a range of 0.107. When compared to the OU model the slowest evolving weapon trait was the anolis lizard ($\sigma^2 = 0.020$) and the fastest was still the bovids ($\sigma^2 = 0.197$), with a range of 0.177. The slowest evolving ornament under the BM model was the agamid lizard dataset ($\sigma^2 = 0.016$), and the fastest evolving ornament was the bird of paradise plumage score ($\sigma^2 = 1.191$), with a range of 1.175. Under the OU model the slowest evolving ornament dataset was the dragonfly ($\sigma^2 = 0.018$) and the fastest was the bird of paradise ($\sigma^2 = 2.910$), with a range of 2.892.

Two of the datasets returned optimisation errors when running the OU model. The error was due to the alpha parameters reaching the upper limit *e*. The datasets affected were the cuckoo plumage score ornament and the stag beetle horn length weapon. Both of these datasets were excluded from the *ratebytree* analysis.

When multiple trait datasets were available for one of the pairs (Table 1) I used the results of the single trait rate analysis to select the most conservative traits (i.e. the slowest evolving ornament and quickest evolving weapon) to present in the main analysis (Table 3). The results of *ratebytree* analyses for all other combinations of weapon and ornament traits are presented as Supplementary Results. For the mammal weapon dataset, the bovid horn length dataset had the fastest rate when compared to artiodactyl tusk length and carnivore canine length (bovid $\sigma^2 = 0.124$; artiodactyl $\sigma^2 = 0.062$; carnivore $\sigma^2 = 0.067$, Table 3) and was therefore selected for the main ratebytree analysis. The ornament datasets selected were dragonfly wing pigmentation trait as its evolutionary rate was slower than the stalk-eyed-fly dragonfly $\sigma^2 = 0.012$; stalk-eyed-flies $\sigma^2 = 0.047$). To match with the ibis beak length three datasets were compared. These were the plumage scores for birds-of-paradise, old world orioles and true finches, of these the old world orioles had the slowest rate and was selected for the main analysis (birds-of-paradise $\sigma^2 = 1.191$; old world orioles $\sigma^2 = 0.036$; true finches $\sigma^2 = 0.313$). Agamid lizard ceratiobranchial length evolved slower than the gliding lizard dewlap area and was therefore selected for the *ratebytree* analysis (agamid lizard $\sigma^2 = 0.016$; gliding lizard $\sigma^2 = 0.042$).

Table 3 – Results of fitting each dataset to the Brownian motion, Ornstein-Uhlenbeck and early burst models. The lowest Akaike information criterion (AIC) scores are highlighted in bold to show the best model for each dataset. The cuckoo and stag beetle dataset have reached the maximum alpha (α) parameter and were not included in later ratebytree analysis.

Taxa	Number of species	Tree height	Brownian motion				Ornstein-Uhlenbeck					Early burst				
			σ^2	z0	log-lik	AIC	α	σ^2	z0	log-lik	AIC	α	σ^2	z0	log-lik	AIC
Carnivore canine length	43	42.99	0.067	0.143	-57.90	119.80	0.081	0.133	-0.046	-53.46	**112.93**	-1.00E-06	0.067	0.143	-57.90	121.80
Artiodactyl tusk length	62	56.37	0.062	0.317	-72.38	**148.76**	0.021	0.077	0.251	-71.66	149.31	-1.00E-06	0.062	0.317	-72.38	150.76
Bovid horn length	116	16.94	0.124	-0.221	-135.30	274.61	0.114	0.197	-0.185	-128.29	**262.59**	-1.00E-06	0.124	-0.221	-135.30	276.61
Stag beetle horn length	26	83.35	0.059	-0.102	-48.25	100.50	2.718	5.228	-2.536E-05	-36.38	**78.77**	-1.00E-06	0.060	-0.102	-48.25	102.50
Leaf-footed bugs hind leg shape	17	28.49	0.060	0.670	-20.31	**44.61**	0.081	0.084	0.505	-19.78	45.56	-1.00E-06	0.059	0.670	-20.31	46.62
Ibis beak length	10	46.77	0.022	0.183	-11.95	**27.91**	0.031	0.028	0.172	-11.91	29.83	-1.00E-06	0.022	0.183	-11.95	29.91
Harvestman fourth coxa length	12	59.30	0.017	-0.318	-13.309	**30.62**	0.008	0.022	-0.280	-13.26	32.51	-1.00E-06	0.017	-0.318	-13.31	32.62
Gallinaceous bird spur length	103	46.52	0.058	-0.389	-127.77	259.54	0.008	0.091	-0.265	-117.37	**240.74**	-1.00E-06	0.058	-0.390	-127.77	261.54
Anolis lizard bite force	27	52.78	0.020	0.094	-34.83	**73.66**	0.051	0.020	0.094	-34.83	75.66	-3.19E-02	0.053	0.134	-34.43	74.86
Primate canine length	100	71.54	0.046	-0.485	-108.85	221.69	0.040	0.068	-0.513	-104.21	**214.43**	-1.00E-06	0.046	-0.485	-108.85	223.70
Bat song features	23	61.66	0.027	-0.470	-29.86	63.71	0.024	0.051	-0.341	-28.39	**62.79**	-1.00E-06	0.027	-0.470	-29.86	65.71
Stalk-eyed-flies eye span	31	45.00	0.047	-0.665	-36.54	**77.09**	0.013	0.056	-0.617	-36.38	78.76	-1.00E-06	0.047	-0.665	-36.54	79.09

Dragonfly posterior wing pigmentation	30	88	0.012	-0.0911	-8.17	**20.33**	0.010	0.018	-0.089	-8.031	22.063	-1.00E-06	0.012	-0.091	-8.17	22.33
Birds-of-paradise plumage score	36	2.97	1.191	0.0669	-53.15	110.30	1.376	2.910	0.018	-49.29	**104.58**	-1.00E-06	1.191	0.067	-53.15	112.30
Cuckoo plumage score	128	12.19	0.819	-0.147	-245.01	494.03	2.718	5.848	0.009	-185.36	**376.72**	-1.00E-06	0.819	-0.147	-245.014	496.03
Old world orioles plumage score	35	37.73	0.036	-0.302	-35.73	**75.46**	0.014	0.044	-0.247	-35.42	76.83	-1.00E-06	0.036	-0.302	-35.73	77.46
True finches plumage score	190	24.50	0.313	0.282	-301.68	607.37	0.265	0.591	0.131	-258.36	**522.72**	-1.00E-06	0.313	0.282	-301.68	609.37
Jumping spider body ornamentation	32	13.93	0.261	-0.021	-50.45	104.90	0.380	0.745	-0.151	-44.02	**94.04**	-1.00E-06	0.261	-0.022	-50.45	106.90
Gallinaceous bird plumage score	62	68.24	0.113	0.233	-104.40	212.80	0.193	0.399	-0.041	-85.52	**177.06**	-1.00E-06	0.113	0.233	-104.40	214.80
Gliding lizard dewlap area	10	37.30	0.042	-0.016	-14.95	33.90	0.126	0.224	-0.017	-13.61	**33.22**	-1.00E-06	0.042	-0.016	-14.95	35.90
Agamid lizard ceratiobranchial length	42	148.52	0.016	-0.139	-61.36	126.73	0.019	0.039	0.010	-58.48	**122.95**	-1.00E-06	0.016	-0.139	-61.37	128.73
Primate ornament score	91	63.64	0.313	-0.186	-134.85	273.70	0.131	0.276	-0.064	-124.26	**254.53**	-1.00E-06	0.153	-0.186	-134.85	275.70

The phylogenies of the paired datasets selected for the main *ratebytree* analysis can be seen in figure 4. The figure shows the diversification of the weapon and ornament traits across the phylogenies. In general, the colour of the phylogenies directly correlated to the extremity of the trait, where red is highly ornamented or weaponed species and blue are species with low to no amount of ornamentation or weapons. However, in the case of the colouration datasets such as gallinaceous birds plumage the scale can be seen as both extremities of the trait on the end of each scale converging to a less ornamented species in the middle (green). The habronattus jumping spider phylogeny also does not fit this format as the more highly ornamented the species is the lower the MDS score is and therefore will be more blue with the more ornamented species.

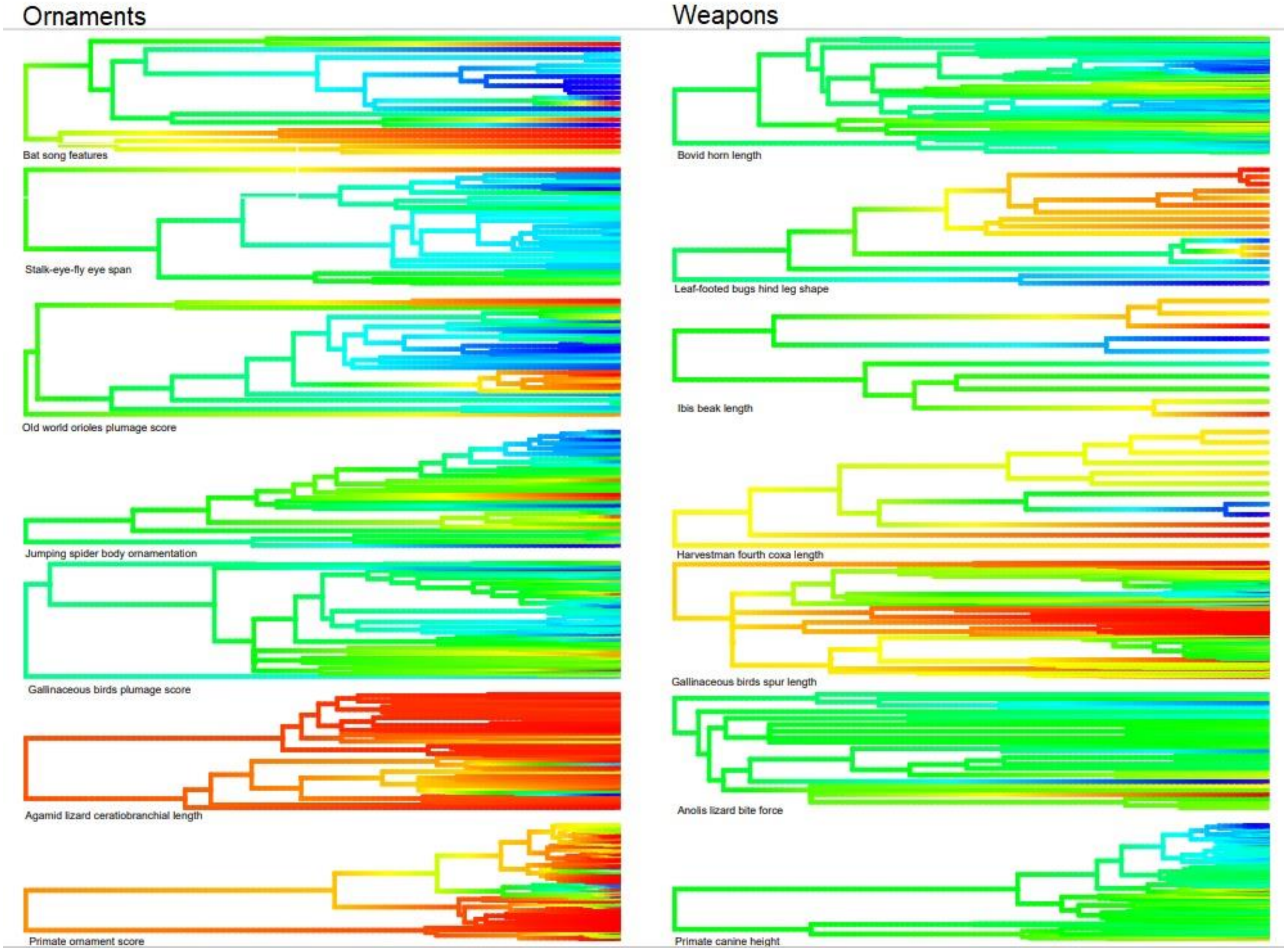

Figure 4 – The phylogenies used in the ratebytree analysis with the weapon and ornament traits plotted along the branches.

As the results of the single trait rate analyses showed some of the datasets best fit a BM model while others best fit an OU model the *ratebytree* analysis was ran twice times using both BM and OU as the underlying model for every permutation of datasets.

Under a BM model the *ratebytree* analysis shows strong support for a model where the rate of evolution is higher in ornaments than weapons (common rate model log-likelihood = -997.19; multiple rate model log-likelihood = -989.28, χ^2P = 6.92E-05, likelihood ratio = 15.83, ornaments σ^2 = 0.107; weapons σ^2 = 0.070).

The *ratebytree* analysis was also run using the OU parameters. The result of this analysis was that ornaments have a higher evolutionary rate than weapons (common rate model log-likelihood = -868.81; multiple rate model log-likelihood = -861.09, χ^2P = 4.42E-04, likelihood ratio = 15.45, ornaments σ^2 = 0.234; weapons σ^2 = 0.116).

The individual rates of trait evolution and the overall faster rate of ornament evolution is presented in figure 5a, which displays the differences between the σ^2 rates of each dataset. Two ornament datasets (jumping spiders and primates) have higher rates than the highest rate of weapon dataset (bovid). The largest difference in rates in figure 5a is between the jumping spider body ornamentation and harvestman fourth coxa length, where the difference is 0.241 (jumping spider σ^2 = 0.261; harvestman σ^2 = 0.020). The slowest rate is the agamid lizard ceratiobranchial length ornament dataset (agamid lizard σ^2 = 0.016).

The rates for the OU single trait analysis can be visualised in figure 5b. The results are similar to the BM model, however there are three ornament datasets (jumping spider, gallinaceous birds and primates) with a higher rate than the highest weapon dataset (bovids). Gallinaceous birds ornament dataset had a higher rate under the OU in comparison to the BM and the dataset fit OU better than BM (BM σ^2 = 0.113, OU σ^2 = 0.399; BM AIC 212.80, OU AIC = 177.04). The largest difference between the rates is still between the jumping spider and the harvestman (difference σ^2 = 0.723; jumping spider σ^2 = 0.745; harvestman σ^2 = 0.022).

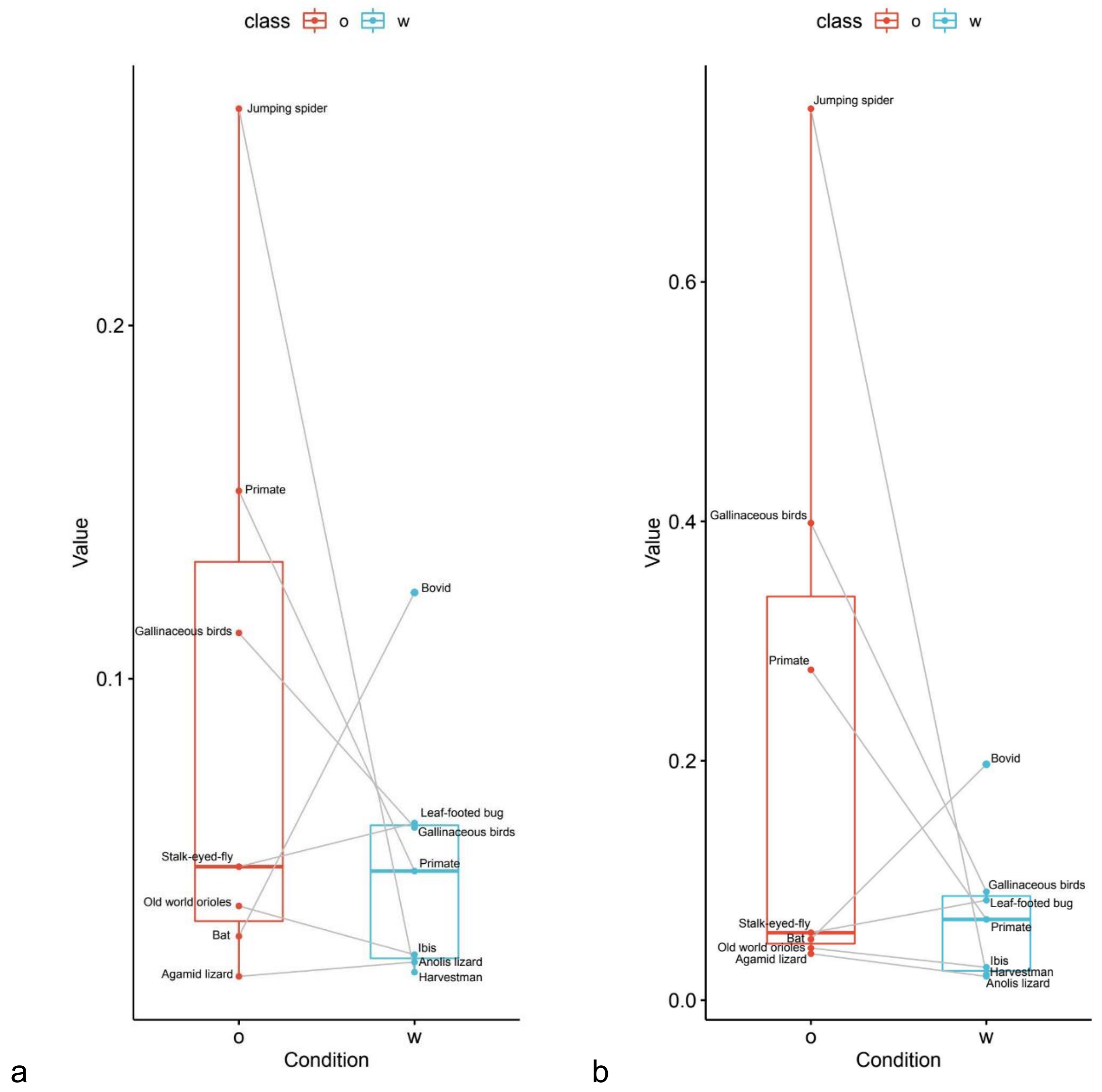

Figure 5 – In both plots ornaments are red and weapons are blue. Each point represents the evolutionary rate of trait dataset. Value is the σ² rate obtained from the single trait analysis. *a: The results of the ratebytree analysis using the BM model. y-axis is from 0 to 0.26. b: The results of the ratebytree analysis using the OU model. y-axis is from 0 to 0.74.*

Discussion

In this thesis I tested the hypothesis that ornaments evolve faster than weapons. I formed pairs of weapon and ornament datasets from related taxa and tested whether the data better supported a single-rate or two-rate model for the evolution of weapons and ornaments. Using this method, it was found that the two-rate model was strongly supported and that ornaments evolve significantly quicker than weapons. The hypothesis was tested under BM and OU models and the result was significant under both models. This result suggests that Fisherian processes are potentially acting on ornament evolution at macroevolutionary scales across taxa *(Fisher, 1915)*.

The results align with the Darwin/Fisher/Lande model of runaway selection *(Fisher, 1915; Fisher, 1930; Lande 1981)* for sexually selected ornaments. The Fisher process is the earliest formal theory for the evolution of sexually selected ornaments. It suggests that there is a positive feedback loop arising from a genetic correlation between male ornament genes and female preference genes that accelerates the rate of trait diversification due to mate preference *(Fisher, 1915; Fisher, 1930; Lande, 1981)*. Preferences for more ornamented traits produce ‘sexy sons’ who in turn have increased mating success (and produce female offspring with stronger preferences) in the next generation. This can lead to the evolution of exaggerated ornaments that are inconsistent with naturally selected traits. While male weapons can also become highly exaggerated, for example through arms-race dynamics *(Dawkins & Krebs 1979)*, because there is no selection on females in a population, the evolutionary rate of weapons is expected to be slower. The current evidence for Fisherian runaway processes is relatively lacking and my results may support the process operating at macroevolutionary scales in diverse taxa. The interaction between natural selection and sexual selection has caused rapid evolution and diversification of sexual traits, especially those that have a role in intersexual competition *(Lande, 1981)*.

The analysis was repeated 96 times with different permutations of weapon and ornament datasets for both the BM and OU models. Under both models every permutation showed that ornaments evolved significantly faster. The repeated outcome in favour of the hypothesis that ornaments evolve quicker than weapons strengthen the results.

Due to the comparative nature of the thesis it is not possible to exclude processes other than Fisherian runaway processes acting on the traits that may generate a pattern of higher rate evolution. The relatively unconstrained trait space of colour or acoustic traits compared to the perhaps generally smaller trait space of weapons has potential to slow the rate of weapon diversification *(Berglund, 2013).*Ornament traits may also have other processes acting upon them by either good gene theory, the handicap principle or sensory processing. The good gene theory can explain the choosiness of females as they select for ornaments where ornament traits correlate directly with male fitness *(Moller & Alatalo, 1999)*. This can also produce runaway evolution. However, this type of effect, where sexually and naturally selected traits are linked, might also be expected to increase the rate of weapon evolution in groups where the weapons are multifunctional, for example having a role in antipredator defence or locomotion, such as mammals, leaf-footed bugs and ibis. The handicap principle may have impacted the results. Under this model species sexually selected traits diverge as individuals are selected for signals that present the greatest handicap, with only high-fitness individuals able to give high-cost signals with honesty maintained by differential costs bourne by individuals l *(Zahavi, 1975)*. As handicap processes would be expected to operate on both signalling using weapons between males *(Somjee et al., 2018)*, and ornament signalling between males and females, it is not obvious why handicap processes would lead to differential rates of evolution between weapons and ornaments. Sensory processing is expected to have impacted the results by defining the trait space, the traits can only evolve as quickly as signal processing systems can evolve *(Endler et al., 2007)*.

The final analysis was run under both BM and OU models. The EB model was tested in initial analysis but was not selected for the final results as none of the datasets fit the model. The EB model is generally best fit to trait that diversified early, and the rates of evolution have slowed over time *(Harmon et al., 2010)*. This does not fit with sexually selected traits due to the constant change in expression of traits through influences such as female choice, competition and environmental fluctuations *(Kirkpatrick, 1982)*. The BM and OU models were both used in the final analysis as some datasets fit BM and some OU. The BM model is a simple model that can capture the evolution of a large range of traits using relatively simple methods *(Wang & Uhlenbeck, 1945)*. The BM model will fit three scenarios of evolution which are either traits have evolved randomly due to genetic drift *(Lande, 1976)* or strong selection that varies in direction is acting upon them *(Hansen & Martins, 1996)*. The OU model adds an additional parameter α, which describes an optimal trait value, to the BM model. Often the OU model fits sexually selected traits well *(Arnold & Houck, 2016)*. This may be because α can account for the role of natural selection in the evolution of sexually selected traits, which can pull traits back from extravagance *(Ho & Ane, 2013)*. These natural selection constraints act on both weapons and ornaments.

Two of the trait datasets did not converge in the OU model. These were the cuckoo plumage score and the stag beetle horn length datasets. Both datasets did not converge as the OU model is bound by α and both datasets reached the limit of the α parameter *(Cooper et al., 2016)*. The lack of convergence in the datasets may be due to the maximum likelihood optimisation algorithm not distinguishing between the α and σ^2 values *(Cooper et al., 2016).* It cannot be known the exact reason they did not converge, but neither datasets were used in the final analysis and therefore will not have impacted the main result.

The bovid horn was the fastest evolving weapon in the group. When compared to the other mammals weapon datasets under BM model the rate is almost twice as fast (Bovid $\sigma^2 = 0.124$; carnivore $\sigma^2 = 0.067$; artiodactyl $\sigma^2 = 0.062$). This fits with the hypothesis as bovid horns are known to function as ornaments as well as weapons *(Manning, 1985)*.

Highly exaggerated sexual ornament and weapon traits may also be under positive selection for other functions such as social signalling, parental care or predator evasion. In any of these cases natural selection for exaggerated ornamental traits may be stronger than sexual selection *(Kelley, 1981),* or it may only weakly oppose it. Acoustic signalling is often used for both social signalling and sexual signalling, birds use their calls to express a wide range of information including, but not limiting to attracting mates *(Price, 2015)*. Although my dataset did not include example of avian calls, bat calls are known for to also have a wide range of functions such as predation and locomotion *(Smotherman et al., 2016)*. This multi-functionality of bat calls may explain the result of how low the rate of evolution the bat song features was when compared to bovid horn length (bat BM $\sigma^2 = 0.027$; bovid BM $\sigma^2 = 0.124$) as other functions selected for, rather than opposed, extreme values.

There were two other pairs where the weapon trait had a higher rate of evolution than the ornament. This was seen comparing the rates of the leaf-footed bug weapon and stalk-eyed-fly ornament, and the anolis lizard weapon and the agamid lizard ornament. In both these instances the weapon trait is used for functions other than just sexual signalling. The leaf-footed bug's weapon is the shape of its hind legs, although the morphological features of its hind legs are used in male-male combat they are also an aid in other aspects of life such a predator evasion *(Emberts et al., 2021)* and therefore may have a stronger selection pressure than the stalk-eyed-flies eyestalks which are purely ornamental and provide no other function *(Lupold et al., 2015)*. The anolis lizard weapon is bite force and is used for predation as well as male-male combat *(Herrel et al., 2007)*, whereas the agamid lizard's ceratiobrancial length is another pure ornament trait with no other know function *(Ord et al., 2015)*. It is possible in both these cases the weapons have natural selection acting on them strongly due to their functions other than just sexual selection. This could increase the evolutionary rate as the intensity of selection is increased and optimal phenotypes may fluctuate more quickly as environments change *(Smith, 1976)*. Alternatively, or additionally, these instances may be examples where the ornament traits have a more constrained trait space than the weapon traits they are paired with*(Rolhausen et al., 2018)*. Eyestalk and ceratobranchial length a unidimensional measures whereas hind-leg shape is a multidimensional trait transformed to a single dimension, and bite force is influenced by changes in multiple morphological traits. This is an indicator that the dimensionality and volume of trait space may be important instead of or as well as the strength of Fisherian processes in influencing the rate of trait evolution *(Rolhausen et al., 2018)*.

When designing the project, it was decided to pair the weapon and ornament datasets. The aim of this was to partially control for factors that may have an influence on the rate of evolution per unit time between datasets, such as the generation time of the taxa. The generation time is important to control for as it can raise heterogeneity in rates by recombination and rates will be faster for taxa with a short generation time e.g. Arthropods, and slower for taxa with long generation times e.g. Mammals. When matching the datasets, the closest related taxa were paired together out of the available datasets. As the pairs are constrained by availability (not all taxa have weapons and/or ornaments) the pairs varied in how closely related they were. For example, gallinaceous bird ornament traits were matched with gallinaceous bird weapon traits, but other datasets such as the habronattus jumping spider ornaments were matched with harvestman weapons where they are different Orders (estimated divergence time from timetree.org = 494 MYA). Pairs may differ more or less in other ways too and this might have affected the rate of evolution of their sexually selected traits. For example, bats and bovids were paired but have a much more different lifestyle to agamid and Anolis lizards, or indeed the included taxa which present both weapons and ornaments (gallinaceous birds and primates). These ecological, physiological and behavioural influences specific to taxa could have drastic effects on the rate of sexually selected trait evolution. For example, in systems where female choice is preferred when compared to where male combat is preferred the mating systems tend to differ. In female choice systems generally monogamy, polyandry and polygynandry mating systems are preferred *(Moller, 1988; Kvarnemo & Simmons, 2013; Fitze et al., 2010)*. In male combat systems polygyny is generally the preferred mating system *(Schwagmeyer, 1988)*. In most of my weapon datasets all the species are in a polygynous mating system where male combat is beneficial for accessing females *(Clutton-Brock, 1985)*.

The ornament and weapon traits are highly multivariate. When analysed each trait was reduced down to one dimension to enable analysis as the *ratebytree* function only accepts univariate traits. Additionally, I decided to standardise all traits so that evolutionary rates were not affected by the scale of trait measurement *(Sokal & Rohlf, 2011)*. Although each trait was standardised this does not account for the relative trait space that may differ between weapons and ornaments. For example, I assume that the bird plumage score datasets have much larger potential trait spaces to evolve in comparison to the ibis beak length dataset which can only evolve in one dimension by getting longer or shorter. For the traits with less trait space to evolve it can be expected for the rate of diversification of traits to slow, even after transformation of multivariate traits to a univariate trait, as there is a constraint on the diversity of the trait *(Rolhausen et al., 2018)*. To address this issue the limit of evolutionary change can be standardised using the rate of ‘trait space saturation’ using fossil records and extant data *(Rolhausen et al., 2018)*. This would place the traits of different taxa on an equivalent scale but allow taxa to differ in the length of the scale.

When measuring the rate of evolution only one tree was used per dataset. This prevents analysis of the role phylogenetic uncertainty about the true evolutionary history in results to be assessed *(Range et al., 2015)*. For some of the taxa tree blocks are available and it would be beneficial to analyse the tree blocks with the *ratebytree* function to obtain distributions for key parameters under alternative phylogenetic hypotheses *(Revell et al., 2018)*.

Traits that show species-level plasticity will have less accurate estimates of rates as plasticity increases. Generally, ornaments have more plasticity than weapons *(Cornwallis & Uller, 2010)*. I could only use specific datasets that fit the criteria to the study and therefore trait plasticity amongst species could not be accounted for. Weapons may not have the same plasticity, plastic weapon traits are highly linked to environmental conditions and during environmental hardship the traits are generally regulated and to reduce cost are less exaggerated *(Zinna et al., 2018)*. This difference in plasticity between weapons and ornaments may have increased the evolutionary rates of ornaments and account for the result. This is because when species-level traits are measured with error, which will increase for plastic traits, rates of evolution on branches will increase.

In some of the datasets analysed the sexual trait was lost in certain species or clades in the taxa. This was more frequent across the weapon datasets than the ornaments and therefore this could reduce the estimate of evolutionary rate in weapons, as seen in figure 4 in the harvestman weapon dataset the trait was lost by a clade. This can potentially add a bias into the results against the weapon dataset and slowing the overall evolutionary rate down *(Derryberry et al., 2011; Cooney et al., 2019)*. To address this potential bias in future I would densely sample morphological traits within clades that still retain the trait of interest and also investigate evolutionary models which allow rate-shift on the phylogeny *(Rabosky et al., 2017)*. The harvestman losing the weapon traits in a large clade may have impacted the results as under the BM model the harvestman had the lowest rate of the weapon datasets and second lowest under the OU model (see table 3).

In future repeats of the analysis, I would adjust some of the methodology. As previously mentioned, I would analyse tree blocks were possible instead of single phylogenies and focus on clades that retain weapon and ornament traits. I would also remove the habronattus jumping spider and harvestman datasets from the analysis. This is because the jumping spider individual rate was a lot higher than the other ornament traits and therefore may have skewed the results.

Conclusion

In this report I was able to test the hypothesis that ornaments evolve faster than weapons *(McCullough et al., 2016)* and the results presented in the study back this hypothesis. The results have potential to support the key sexual selection mechanism theory of Fisherian runaway process on a macroevolutionary scale across diverse taxon. The effect was present across both Brownian motion and Ornstein-Uhlenbeck models of evolution. There may be other sexual selection process acting upon the results also, but there is strong evidence for Fisher processes. Some potential extensions of the study to strengthen the results further would be beneficial, though this is one the limited studies with evidence suggesting Fisher processes in sexual selection.

Appendix A - Output of the *ratebytree* function with results of all 96 iterations under BM. Abbreviations are SEF = Stalk-eyed-fly; OWO = Old world orioles; AgL = Agamid lizard; Bo = Bovids; SB = Stag beetle; GL = Gliding lizard; Df = Dragonfly; LFB = Leaf-footed bug; Ca = Carnivore; Ar = Artiodactyl; TF = True finches; BOP = Birds of paradise; Cu = Cuckoo. For traits that didn't converge the convergence = 52.

Dataset combination	Common rate		Multiple rate				Common logL	multi_ ogL	LRT	P chisq	Convergencve	
	sig2	SE.sig2	O sig2	W sig2	O SE.sig2	W SE.sig2					common	multi
SEF OWO AgL Bo LFB	0.087	0.0046	0.107	0.070	0.0085	0.0050	-997.19	-989.28	15.83	6.92E-05	0	0
SEF OWO AgL Bo SB	0.086	0.0046	0.107	0.070	0.0085	0.0050	-1025.36	-1017.25	16.23	5.61E-05	0	0
Df OWO AgL Bo LFB	0.088	0.0047	0.111	0.070	0.0091	0.0050	-970.48	-961.52	17.91	2.32E-05	0	0
Df OWO AgL Bo SB	0.087	0.0047	0.111	0.070	0.0091	0.0050	-998.66	-989.50	18.33	1.85E-05	0	0
SEF OWO GL Bo LFB	0.090	0.0049	0.118	0.070	0.0098	0.0050	-932.52	-921.20	22.64	1.95E-06	0	0
SEF OWO GL Bo SB	0.090	0.0049	0.118	0.070	0.0098	0.0050	-960.75	-949.18	23.15	1.50E-06	0	0
SEF OWO AgL Ca LFB	0.084	0.0047	0.107	0.060	0.0085	0.0048	-936.18	-923.51	25.34	4.80E-07	0	0
Df OWO GL Bo LFB	0.092	0.0051	0.123	0.070	0.0107	0.0050	-905.64	-892.88	25.51	4.39E-07	0	0
SEF OWO AgL Ca SB	0.084	0.0047	0.107	0.061	0.0085	0.0048	-964.31	-951.44	25.72	3.94E-07	0	0
Df OWO GL Bo SB	0.091	0.0050	0.123	0.070	0.0107	0.0050	-933.88	-920.85	26.06	3.31E-07	0	0
Df OWO AgL Ca LFB	0.085	0.0049	0.111	0.060	0.0091	0.0048	-909.58	-895.75	27.66	1.45E-07	0	0
Df OWO AgL Ca SB	0.085	0.0048	0.111	0.061	0.0091	0.0048	-937.73	-923.69	28.07	1.17E-07	0	0
SEF OWO GL Ca LFB	0.088	0.0051	0.118	0.060	0.0098	0.0048	-871.94	-855.43	33.02	9.14E-09	0	0
SEF OWO GL Ca SB	0.087	0.0050	0.118	0.061	0.0098	0.0048	-900.13	-883.37	33.51	7.08E-09	0	0
Df OWO GL Ca LFB	0.089	0.0052	0.123	0.060	0.0107	0.0048	-845.17	-827.11	36.12	1.86E-09	52	0
Df OWO GL Ca SB	0.089	0.0052	0.123	0.061	0.0107	0.0048	-873.37	-855.05	36.65	1.41E-09	0	0
SEF OWO AgL Ar SB	0.077	0.0043	0.107	0.050	0.0085	0.0038	-957.65	-933.92	47.45	5.65E-12	0	0
SEF OWO AgL Ar LFB	0.078	0.0043	0.107	0.049	0.0085	0.0038	-929.60	-905.87	47.45	5.64E-12	0	0

Df OWO AgL Ar LFB	0.078	0.0044	0.111	0.049	0.0091	0.0038	-903.26	-878.12	50.29	1.32E-12	52	52
Df OWO AgL Ar SB	0.078	0.0044	0.111	0.050	0.0091	0.0038	-931.32	-906.17	50.31	1.32E-12	0	0
SEF OWO GL Ar LFB	0.081	0.0046	0.118	0.049	0.0098	0.0038	-866.46	-837.80	57.32	3.70E-14	0	0
SEF OWO GL Ar SB	0.081	0.0046	0.118	0.050	0.0098	0.0038	-894.55	-865.85	57.40	3.55E-14	52	0
Df OWO GL Ar LFB	0.082	0.0048	0.123	0.049	0.0107	0.0038	-839.98	-809.47	61.02	5.65E-15	0	0
Df OWO GL Ar SB	0.082	0.0047	0.123	0.050	0.0107	0.0038	-868.09	-837.53	61.13	5.35E-15	0	52
SEF TF AgL Bo LFB	0.139	0.0067	0.195	0.070	0.0126	0.0050	-1327.86	-1276.21	103.29	2.89E-24	0	0
SEF TF AgL Bo SB	0.138	0.0066	0.195	0.070	0.0126	0.0050	-1356.94	-1304.18	105.52	9.42E-25	0	0
Df TF AgL Bo LFB	0.141	0.0069	0.202	0.070	0.0134	0.0050	-1298.56	-1244.31	108.51	2.08E-25	0	0
Df TF AgL Bo SB	0.140	0.0068	0.202	0.070	0.0134	0.0050	-1327.69	-1272.28	110.81	6.52E-26	52	0
SEF TF GL Bo LFB	0.144	0.0071	0.208	0.070	0.0140	0.0050	-1256.38	-1199.41	113.93	1.35E-26	0	0
SEF TF AgL Ca LFB	0.141	0.0071	0.195	0.060	0.0126	0.0048	-1267.42	-1210.44	113.96	1.33E-26	0	0
SEF TF GL Bo SB	0.143	0.0070	0.208	0.070	0.0140	0.0050	-1285.55	-1227.38	116.33	4.02E-27	0	0
SEF TF AgL Ca SB	0.140	0.0070	0.195	0.061	0.0126	0.0048	-1296.54	-1238.38	116.33	4.02E-27	0	0
Df TF AgL Ca LFB	0.144	0.0073	0.202	0.060	0.0134	0.0048	-1238.00	-1178.54	118.92	1.09E-27	0	0
Df TF GL Bo LFB	0.146	0.0073	0.216	0.070	0.0149	0.0050	-1226.84	-1166.95	119.78	7.07E-28	0	0
Df TF AgL Ca SB	0.143	0.0073	0.201	0.061	0.0134	0.0048	-1267.17	-1206.48	121.39	3.15E-28	0	0
Df TF GL Bo SB	0.145	0.0072	0.216	0.070	0.0149	0.0050	-1256.06	-1194.92	122.27	2.02E-28	0	0
SEF TF GL Ca LFB	0.147	0.0075	0.208	0.060	0.0140	0.0048	-1195.65	-1133.64	124.03	8.29E-29	0	0
SEF TF GL Ca SB	0.146	0.0074	0.208	0.061	0.0140	0.0048	-1224.88	-1161.58	126.60	2.27E-29	0	52
SEF BOP AgL Bo LFB	0.146	0.0077	0.236	0.070	0.0186	0.0050	-1134.70	-1071.35	126.70	2.16E-29	0	0
SEF BOP AgL Bo SB	0.144	0.0076	0.236	0.070	0.0186	0.0050	-1163.91	-1099.32	129.16	6.25E-30	0	0

Df TF GL Ca LFB	0.150	0.0078	0.216	0.060	0.0149	0.0048	-1165.97	-1101.18	129.58	5.07E-30	0	0
Df TF GL Ca SB	0.148	0.0077	0.216	0.061	0.0149	0.0048	-1195.24	-1129.12	132.25	1.32E-30	0	0
Df BOP AgL Bo LFB	0.148	0.0080	0.250	0.070	0.0205	0.0050	-1105.07	-1037.72	134.70	3.84E-31	0	0
SEF BOP AgL Ca LFB	0.149	0.0084	0.236	0.060	0.0186	0.0048	-1073.86	-1005.58	136.55	1.51E-31	0	0
Df BOP AgL Bo SB	0.147	0.0079	0.250	0.070	0.0205	0.0050	-1134.32	-1065.69	137.26	1.06E-31	0	0
SEF BOP AgL Ca SB	0.148	0.0083	0.236	0.061	0.0186	0.0048	-1103.13	-1033.52	139.21	3.96E-32	0	0
SEF BOP GL Bo LFB	0.152	0.0083	0.261	0.070	0.0217	0.0050	-1062.45	-991.33	142.25	8.58E-33	0	0
Df BOP AgL Ca LFB	0.153	0.0087	0.250	0.060	0.0205	0.0048	-1044.03	-971.95	144.17	3.26E-33	0	0
SEF BOP GL Bo SB	0.151	0.0082	0.261	0.070	0.0217	0.0050	-1091.77	-1019.30	144.93	2.22E-33	0	0
Df BOP AgL Ca SB	0.151	0.0086	0.250	0.061	0.0205	0.0048	-1073.36	-999.89	146.95	8.06E-34	0	0
SEF BOP GL Ca LFB	0.157	0.0090	0.261	0.060	0.0217	0.0048	-1001.19	-925.56	151.26	9.20E-35	0	0
Df BOP GL Bo LFB	0.155	0.0086	0.279	0.070	0.0242	0.0050	-1032.51	-956.76	151.49	8.19E-35	0	0
SEF BOP GL Ca SB	0.155	0.0089	0.261	0.061	0.0217	0.0048	-1030.58	-953.50	154.17	2.12E-35	0	0
Df BOP GL Bo SB	0.154	0.0085	0.279	0.070	0.0242	0.0050	-1061.88	-984.73	154.29	2.00E-35	0	0
SEF TF AgL Ar LFB	0.135	0.0067	0.195	0.049	0.0126	0.0038	-1272.15	-1192.80	158.69	2.19E-36	0	0
Df BOP GL Ca LFB	0.161	0.0094	0.279	0.060	0.0242	0.0048	-971.01	-890.99	160.03	1.11E-36	0	52
SEF TF AgL Ar SB	0.134	0.0066	0.195	0.050	0.0126	0.0038	-1301.16	-1220.85	160.61	8.31E-37	0	0
Df BOP GL Ca SB	0.159	0.0093	0.279	0.061	0.0242	0.0048	-1000.47	-918.93	163.08	2.40E-37	0	0
Df TF AgL Ar LFB	0.137	0.0069	0.202	0.049	0.0134	0.0038	-1243.04	-1160.90	164.27	1.32E-37	0	0
Df TF AgL Ar SB	0.136	0.0069	0.202	0.050	0.0134	0.0038	-1272.09	-1188.96	166.27	4.82E-38	0	0
SEF TF GL Ar LFB	0.140	0.0071	0.208	0.049	0.0140	0.0038	-1201.06	-1116.00	170.12	6.96E-39	0	0
SEF TF GL Ar SB	0.139	0.0070	0.208	0.050	0.0140	0.0038	-1230.17	-1144.06	172.23	2.41E-39	0	0

Df TF GL Ar LFB	0.143	0.0074	0.216	0.049	0.0149	0.0038	-1171.70	-1083.54	176.31	3.09E-40	52	0
Df TF GL Ar SB	0.142	0.0073	0.216	0.050	0.0149	0.0038	-1200.85	-1111.60	178.51	1.02E-40	0	0
SEF BOP AgL Ar LFB	0.141	0.0078	0.236	0.049	0.0186	0.0038	-1079.50	-987.94	183.11	1.02E-41	0	0
SEF BOP AgL Ar SB	0.140	0.0077	0.236	0.050	0.0186	0.0038	-1108.63	-1016.00	185.26	3.45E-42	0	0
Df BOP AgL Ar LFB	0.144	0.0081	0.250	0.049	0.0205	0.0038	-1050.06	-954.31	191.49	1.50E-43	0	52
Df BOP AgL Ar SB	0.143	0.0080	0.250	0.050	0.0205	0.0038	-1079.24	-982.37	193.75	4.82E-44	0	0
SEF BOP GL Ar LFB	0.148	0.0084	0.261	0.049	0.0217	0.0038	-1007.65	-907.92	199.46	2.74E-45	0	0
SEF BOP GL Ar SB	0.147	0.0083	0.261	0.050	0.0217	0.0038	-1036.90	-935.98	201.85	8.23E-46	0	0
Df BOP GL Ar LFB	0.152	0.0088	0.279	0.049	0.0242	0.0038	-977.88	-873.36	209.05	2.21E-47	0	0
Df BOP GL Ar SB	0.150	0.0086	0.279	0.050	0.0242	0.0038	-1007.19	-901.41	211.57	6.25E-48	0	0
SEF Cu AgL Bo LFB	0.206	0.0103	0.334	0.070	0.0232	0.0050	-1393.22	-1284.05	218.35	2.08E-49	0	0
SEF Cu AgL Ca LFB	0.216	0.0113	0.334	0.060	0.0232	0.0048	-1327.76	-1218.28	218.97	1.52E-49	0	0
SEF Cu AgL Bo SB	0.205	0.0102	0.334	0.070	0.0232	0.0050	-1423.43	-1312.02	222.82	2.19E-50	0	0
SEF Cu AgL Ca SB	0.214	0.0111	0.334	0.061	0.0232	0.0048	-1358.11	-1246.21	223.79	1.35E-50	0	0
Df Cu AgL Ca LFB	0.221	0.0118	0.350	0.060	0.0251	0.0048	-1295.06	-1181.51	227.09	2.57E-51	0	0
Df Cu AgL Bo LFB	0.211	0.0107	0.350	0.070	0.0251	0.0050	-1360.89	-1247.28	227.22	2.41E-51	0	0
Df Cu AgL Bo SB	0.209	0.0106	0.350	0.070	0.0251	0.0050	-1391.17	-1275.26	231.83	2.38E-52	0	0
Df Cu AgL Ca SB	0.219	0.0116	0.350	0.061	0.0251	0.0048	-1325.48	-1209.45	232.06	2.12E-52	0	0
SEF Cu GL Ca LFB	0.225	0.0121	0.361	0.060	0.0261	0.0048	-1249.57	-1133.08	232.97	1.34E-52	0	0
SEF Cu GL Bo LFB	0.215	0.0110	0.361	0.070	0.0261	0.0050	-1315.73	-1198.86	233.74	9.12E-53	0	0
SEF Cu GL Ca SB	0.223	0.0119	0.361	0.061	0.0261	0.0048	-1280.05	-1161.02	238.06	1.04E-53	0	0
SEF Cu GL Bo SB	0.213	0.0108	0.361	0.070	0.0261	0.0050	-1346.06	-1226.83	238.46	8.52E-54	0	0

Df Cu GL Ca LFB	0.231	0.0126	0.380	0.060	0.0284	0.0048	-1216.49	-1095.54	241.89	1.52E-54	0	0
Df Cu GL Bo LFB	0.219	0.0114	0.380	0.070	0.0284	0.0050	-1283.07	-1161.31	243.50	6.77E-55	0	0
Df Cu GL Ca SB	0.229	0.0124	0.380	0.061	0.0284	0.0048	-1247.06	-1123.48	247.15	1.09E-55	0	0
Df Cu GL Bo SB	0.218	0.0112	0.380	0.070	0.0284	0.0050	-1313.47	-1189.29	248.37	5.89E-56	0	0
SEF Cu AgL Ar LFB	0.207	0.0107	0.334	0.049	0.0232	0.0038	-1339.41	-1200.64	277.55	2.57E-62	0	0
SEF Cu AgL Ar SB	0.205	0.0106	0.334	0.050	0.0232	0.0038	-1369.63	-1228.69	281.88	2.92E-63	0	0
Df Cu AgL Ar LFB	0.212	0.0112	0.350	0.049	0.0251	0.0038	-1307.05	-1163.88	286.34	3.12E-64	0	0
Df Cu AgL Ar SB	0.210	0.0110	0.350	0.050	0.0250	0.0038	-1337.34	-1191.93	290.82	3.29E-65	0	0
SEF Cu GL Ar LFB	0.216	0.0114	0.361	0.049	0.0261	0.0038	-1261.84	-1115.45	292.78	1.23E-65	0	0
SEF Cu GL Ar SB	0.214	0.0113	0.361	0.050	0.0261	0.0038	-1292.19	-1143.50	297.38	1.23E-66	0	0
Df Cu GL Ar LFB	0.221	0.0119	0.380	0.049	0.0284	0.0038	-1229.12	-1077.91	302.42	9.80E-68	0	0
Df Cu GL Ar SB	0.219	0.0117	0.380	0.050	0.0284	0.0038	-1259.55	-1105.96	307.17	9.02E-69	0	0

Appendix B - Output of the *ratebytree* function with results of all 96 iterations under OU. Abbreviations are SEF = Stalk-eyed-fly; OWO = Old world orioles; AgL = Agamid lizard; Bo = Bovids; SB = Stag beetle; GL = Gliding lizard; Df = Dragonfly; LFB = Leaf-footed bug; Ca = Carnivore; Ar = Artiodactyl; TF = True finches; BOP = Birds of paradise; Cu = Cuckoo. For traits that didn't converge the convergence = 52.

Dataset combinations	Common rate				Multiple rate								Common logL	Multi logL	LRT	P chisq	Convergence	
	sig2	SE.sig2	alpha	SE.alpha	O sig2	W sig2	O SE.sig2	W SE.sig2	O alpha	W alpha	O SE.alpha	W SE.alpha					common	multi
SEF OWO AgL Bo SB	0.161	0.015	0.081	0.009	0.234	0.122	0.038	0.014	0.110	0.066	0.021	0.0097	-886.15	-879.54	13.22	1.35E-03	0	0
SEF OWO GL Bo SB	0.163	0.015	0.082	0.009	0.235	0.122	0.038	0.014	0.110	0.066	0.022	0.0097	-840.90	-834.10	13.60	1.11E-03	0	0
Df OWO AgL Bo SB	0.164	0.015	0.084	0.009	0.245	0.122	0.041	0.014	0.119	0.066	0.022	0.0097	-886.22	-879.08	14.29	7.90E-04	0	0
Df OWO GL Bo SB	0.165	0.015	0.085	0.009	0.246	0.122	0.040	0.014	0.119	0.066	0.023	0.0097	-840.95	-833.65	14.60	6.75E-04	0	0
SEF OWO AgL Bo LFB	0.157	0.014	0.078	0.009	0.234	0.116	0.038	0.013	0.110	0.062	0.021	0.0093	-868.81	-861.09	15.45	4.42E-04	0	0
SEF OWO GL Bo LFB	0.158	0.014	0.079	0.009	0.235	0.116	0.038	0.013	0.110	0.062	0.022	0.0093	-823.59	-815.65	15.89	3.55E-04	0	0
Df OWO AgL Bo LFB	0.159	0.014	0.081	0.009	0.245	0.116	0.041	0.013	0.119	0.062	0.022	0.0093	-868.96	-860.63	16.67	2.40E-04	0	0
Df OWO GL Bo LFB	0.160	0.014	0.082	0.009	0.246	0.116	0.040	0.013	0.119	0.062	0.023	0.0093	-823.72	-815.20	17.04	1.99E-04	0	0
SEF OWO AgL Ca SB	0.153	0.015	0.077	0.009	0.234	0.089	0.038	0.012	0.110	0.050	0.021	0.0086	-809.14	-797.06	24.17	5.65E-06	0	0
SEF OWO GL Ca SB	0.154	0.015	0.078	0.009	0.235	0.089	0.038	0.012	0.110	0.050	0.022	0.0086	-763.94	-751.62	24.63	4.48E-06	0	0

Df OWO AgL Ca SB	0.156	0.015	0.080	0.009	0.245	0.089	0.041	0.012	0.119	0.050	0.022	0.0086	-809.31	-796.60	25.41	3.04E-06	0	0
Df OWO GL Ca SB	0.157	0.016	0.081	0.009	0.246	0.089	0.040	0.012	0.119	0.050	0.023	0.0086	-764.07	-751.17	25.79	2.51E-06	0	0
SEF OWO AgL Ar SB	0.145	0.014	0.071	0.008	0.234	0.083	0.038	0.010	0.110	0.043	0.021	0.0076	-831.46	-817.06	28.81	5.56E-07	0	0
SEF OWO AgL Ca LFB	0.147	0.014	0.074	0.009	0.234	0.083	0.039	0.010	0.110	0.046	0.021	0.0082	-791.59	-777.15	28.87	5.39E-07	0	0
SEF OWO GL Ca LFB	0.149	0.014	0.075	0.009	0.235	0.083	0.038	0.010	0.110	0.046	0.022	0.0082	-746.42	-731.72	29.41	4.11E-07	0	0
SEF OWO GL Ar SB	0.146	0.014	0.072	0.009	0.235	0.083	0.038	0.010	0.110	0.043	0.022	0.0076	-786.33	-771.62	29.42	4.09E-07	0	0
Df OWO AgL Ca LFB	0.150	0.015	0.077	0.009	0.245	0.083	0.041	0.010	0.119	0.046	0.022	0.0082	-791.84	-776.69	30.28	2.65E-07	0	0
Df OWO AgL Ar SB	0.147	0.014	0.074	0.009	0.245	0.083	0.041	0.010	0.119	0.043	0.022	0.0076	-831.83	-816.60	30.46	2.43E-07	0	0
Df OWO GL Ca LFB	0.151	0.015	0.078	0.009	0.246	0.083	0.040	0.010	0.119	0.046	0.022	0.0082	-746.63	-731.26	30.74	2.11E-07	0	0
Df OWO GL Ar SB	0.149	0.014	0.075	0.009	0.246	0.083	0.040	0.010	0.119	0.043	0.022	0.0076	-786.66	-771.17	31.00	1.86E-07	0	0
SEF OWO AgL Ar LFB	0.140	0.013	0.069	0.008	0.234	0.077	0.038	0.009	0.110	0.040	0.021	0.0074	-813.67	-796.78	33.78	4.62E-08	0	0
SEF OWO GL Ar LFB	0.141	0.013	0.069	0.008	0.235	0.077	0.038	0.009	0.110	0.040	0.022	0.0074	-768.58	-751.34	34.48	3.26E-08	0	0
Df OWO AgL Ar LFB	0.142	0.014	0.071	0.008	0.245	0.077	0.041	0.009	0.119	0.040	0.022	0.0074	-814.13	-796.32	35.62	1.84E-08	0	0
Df OWO GL Ar LFB	0.144	0.014	0.072	0.008	0.246	0.077	0.040	0.009	0.119	0.040	0.023	0.0074	-769.01	-750.89	36.24	1.35E-08	0	0
SEF TF GL Bo SB	0.294	0.025	0.146	0.014	0.485	0.122	0.064	0.014	0.231	0.066	0.033	0.0097	-1085.77	-1053.59	64.38	1.05E-14	0	0
SEF TF AgL Bo SB	0.294	0.025	0.146	0.014	0.485	0.122	0.064	0.014	0.232	0.066	0.033	0.0097	-1131.22	-1099.02	64.39	1.04E-14	0	0

Df TF GL Bo SB	0.296	0.025	0.148	0.014	0.482	0.122	0.062	0.014	0.231	0.066	0.032	0.0097	-1084.93	-1052.63	64.60	9.37E-15	0	0
Df TF AgL Bo SB	0.296	0.025	0.148	0.014	0.482	0.122	0.062	0.014	0.232	0.066	0.032	0.0097	-1130.37	-1098.06	64.62	9.30E-15	0	0
SEF TF GL Bo LFB	0.289	0.025	0.143	0.014	0.485	0.116	0.064	0.013	0.231	0.062	0.033	0.0093	-1070.33	-1035.13	70.40	5.17E-16	0	0
SEF TF AgL Bo LFB	0.289	0.025	0.143	0.014	0.485	0.116	0.064	0.013	0.232	0.062	0.033	0.0093	-1115.77	-1080.57	70.40	5.15E-16	0	0
Df TF GL Bo LFB	0.291	0.025	0.145	0.014	0.482	0.116	0.062	0.013	0.231	0.062	0.032	0.0093	-1069.51	-1034.18	70.66	4.53E-16	0	0
Df TF AgL Bo LFB	0.291	0.025	0.145	0.014	0.482	0.116	0.062	0.013	0.232	0.062	0.032	0.0093	-1114.95	-1079.61	70.68	4.50E-16	0	0
SEF TF GL Ca SB	0.307	0.028	0.150	0.015	0.485	0.089	0.064	0.012	0.231	0.050	0.033	0.0086	-1008.51	-971.11	74.79	5.74E-17	0	0
SEF TF AgL Ca SB	0.307	0.028	0.150	0.015	0.484	0.089	0.064	0.012	0.232	0.050	0.033	0.0086	-1053.95	-1016.55	74.81	5.70E-17	0	0
Df TF GL Ca SB	0.309	0.028	0.152	0.015	0.482	0.089	0.062	0.012	0.231	0.050	0.032	0.0086	-1007.66	-970.15	75.00	5.17E-17	0	0
Df TF AgL Ca SB	0.309	0.028	0.152	0.015	0.482	0.089	0.062	0.012	0.232	0.050	0.032	0.0086	-1053.10	-1015.59	75.02	5.12E-17	0	0
SEF TF GL Ca LFB	0.301	0.028	0.147	0.015	0.484	0.083	0.064	0.010	0.231	0.046	0.033	0.0082	-993.15	-951.20	83.90	6.04E-19	0	0
SEF TF AgL Ca LFB	0.301	0.028	0.147	0.015	0.485	0.083	0.064	0.010	0.232	0.046	0.033	0.0082	-1038.60	-996.64	83.92	5.99E-19	0	0
Df TF GL Ca LFB	0.303	0.028	0.149	0.015	0.482	0.083	0.062	0.010	0.231	0.046	0.032	0.0082	-992.32	-950.25	84.15	5.32E-19	0	0
Df TF AgL Ca LFB	0.303	0.028	0.149	0.015	0.482	0.083	0.062	0.010	0.232	0.046	0.032	0.0082	-1037.77	-995.68	84.17	5.27E-19	0	0
SEF TF GL Ar SB	0.296	0.027	0.143	0.014	0.485	0.083	0.064	0.010	0.231	0.043	0.033	0.0076	-1034.62	-991.10	87.04	1.26E-19	0	0
SEF TF AgL Ar SB	0.296	0.027	0.143	0.014	0.485	0.083	0.064	0.010	0.232	0.043	0.033	0.0076	-1080.07	-1036.54	87.07	1.24E-19	0	0
Df TF GL Ar SB	0.298	0.027	0.145	0.014	0.482	0.083	0.062	0.010	0.231	0.043	0.032	0.0076	-1033.84	-990.15	87.39	1.06E-19	0	0
Df TF AgL Ar SB	0.298	0.027	0.145	0.014	0.482	0.083	0.062	0.010	0.232	0.043	0.032	0.0076	-1079.29	-1035.58	87.41	1.04E-19	0	0
Df BOP GL Bo SB	0.337	0.034	0.163	0.018	0.982	0.122	0.256	0.014	0.473	0.066	0.132	0.0097	-900.08	-853.53	93.10	6.07E-21	0	0
Df BOP AgL Bo SB	0.337	0.035	0.163	0.018	0.984	0.122	0.257	0.014	0.476	0.066	0.133	0.0097	-945.53	-898.95	93.16	5.89E-21	0	0
SEF BOP GL Bo SB	0.335	0.034	0.161	0.018	1.047	0.122	0.285	0.014	0.506	0.066	0.148	0.0097	-900.96	-853.90	94.13	3.63E-21	0	0
SEF BOP AgL Bo SB	0.335	0.035	0.161	0.018	1.048	0.122	0.286	0.014	0.509	0.066	0.148	0.0097	-946.41	-899.31	94.21	3.49E-21	0	0

SEF TF GL Ar LFB	0.290	0.026	0.140	0.014	0.485	0.077	0.064	0.009	0.231	0.039	0.033	0.0074	-1019.17	-970.83	96.68	1.01E-21	0	0
SEF TF AgL Ar LFB	0.290	0.026	0.140	0.014	0.485	0.077	0.064	0.009	0.232	0.040	0.033	0.0074	-1064.62	-1016.27	96.71	1.00E-21	0	0
Df TF GL Ar LFB	0.293	0.026	0.142	0.014	0.482	0.077	0.062	0.009	0.231	0.039	0.032	0.0074	-1018.41	-969.87	97.08	8.32E-22	0	0
Df TF AgL Ar LFB	0.292	0.026	0.142	0.014	0.482	0.077	0.062	0.009	0.232	0.040	0.032	0.0074	-1063.86	-1015.31	97.10	8.21E-22	0	0
Df BOP GL Bo LFB	0.330	0.033	0.159	0.018	0.983	0.116	0.256	0.013	0.473	0.062	0.133	0.0093	-884.93	-835.08	99.70	2.24E-22	0	0
Df BOP AgL Bo LFB	0.330	0.033	0.159	0.018	0.984	0.116	0.256	0.013	0.475	0.062	0.132	0.0093	-930.38	-880.49	99.76	2.17E-22	0	0
SEF BOP GL Bo LFB	0.328	0.033	0.157	0.018	1.048	0.116	0.286	0.013	0.507	0.062	0.149	0.0093	-885.78	-835.44	100.68	1.37E-22	0	0
SEF BOP AgL Bo LFB	0.328	0.033	0.157	0.018	1.047	0.116	0.285	0.013	0.509	0.062	0.148	0.0093	-931.24	-880.86	100.76	1.32E-22	0	0
Df BOP GL Ca SB	0.367	0.043	0.173	0.022	0.981	0.089	0.255	0.012	0.472	0.050	0.132	0.0086	-821.78	-771.05	101.45	9.33E-23	0	0
Df BOP AgL Ca SB	0.367	0.043	0.174	0.022	0.979	0.089	0.254	0.012	0.473	0.050	0.131	0.0086	-867.24	-816.47	101.54	8.94E-23	0	0
SEF BOP GL Ca SB	0.364	0.043	0.171	0.022	1.046	0.089	0.285	0.012	0.506	0.050	0.148	0.0086	-822.67	-771.42	102.51	5.50E-23	0	0
SEF BOP AgL Ca SB	0.364	0.043	0.172	0.022	1.047	0.089	0.285	0.012	0.508	0.050	0.148	0.0086	-868.14	-816.83	102.61	5.23E-23	0	0
Df BOP GL Ca LFB	0.357	0.041	0.168	0.021	0.981	0.083	0.254	0.010	0.472	0.046	0.132	0.0082	-806.78	-751.14	111.27	6.89E-25	0	0
Df BOP AgL Ca LFB	0.357	0.041	0.169	0.021	0.984	0.083	0.256	0.010	0.475	0.046	0.132	0.0082	-852.24	-796.56	111.36	6.59E-25	0	0
SEF BOP GL Ca LFB	0.355	0.041	0.166	0.021	1.051	0.083	0.288	0.010	0.508	0.046	0.150	0.0082	-807.65	-751.51	112.29	4.15E-25	0	0
SEF BOP AgL Ca LFB	0.355	0.041	0.167	0.021	1.053	0.083	0.289	0.010	0.511	0.046	0.150	0.0082	-853.12	-796.92	112.39	3.93E-25	0	0
Df BOP GL Ar SB	0.349	0.040	0.162	0.020	0.978	0.083	0.253	0.010	0.470	0.043	0.131	0.0076	-848.50	-791.05	114.91	1.12E-25	0	0
Df BOP AgL Ar SB	0.348	0.040	0.163	0.020	0.977	0.083	0.252	0.010	0.472	0.043	0.130	0.0076	-893.97	-836.46	115.02	1.06E-25	0	0
SEF BOP GL Ar SB	0.346	0.040	0.160	0.020	1.049	0.083	0.287	0.010	0.507	0.043	0.149	0.0076	-849.33	-791.41	115.84	7.02E-26	0	0

SEF BOP AgL Ar SB	0.345	0.040	0.161	0.020	1.047	0.083	0.285	0.010	0.508	0.043	0.148	0.0076	-894.81	-836.83	115.97	6.56E-26	0	0
Df BOP GL Ar LFB	0.339	0.038	0.158	0.019	0.984	0.077	0.257	0.009	0.474	0.040	0.133	0.0074	-833.38	-770.77	125.22	6.45E-28	0	0
Df BOP AgL Ar LFB	0.339	0.038	0.158	0.019	0.981	0.077	0.255	0.009	0.474	0.040	0.132	0.0074	-878.86	-816.19	125.34	6.07E-28	0	0
SEF BOP GL Ar LFB	0.336	0.038	0.155	0.019	1.047	0.077	0.286	0.009	0.507	0.040	0.149	0.0074	-834.18	-771.14	126.09	4.16E-28	0	0
SEF BOP AgL Ar LFB	0.336	0.038	0.156	0.019	1.045	0.077	0.284	0.009	0.507	0.040	0.147	0.0074	-879.67	-816.55	126.24	3.87E-28	0	0
Df Cu GL Ca SB	59936.340	NaN	30949.600	NaN	74.797	0.089	91.084	0.012	38.130	0.050	46.506	0.0086	-980.53	-907.32	146.42	1.60E-32	0	0
Df Cu AgL Ca SB	119.943	184.229	61.166	93.978	241.178	0.089	NaN	0.012	119.452	0.050	NaN	0.0086	-1025.97	-952.65	146.63	1.44E-32	0	1
SEF Cu GL Ca SB	127.105	202.193	64.870	103.207	255.217	0.089	2909.805	0.012	127.456	0.050	1423.869	0.0086	-980.55	-907.21	146.69	1.40E-32	0	0
SEF Cu AgL Ca SB	118.191	180.019	60.263	91.803	236.649	0.089	752.231	0.012	119.729	0.050	378.415	0.0086	-1025.97	-952.58	146.78	1.34E-32	0	0
Df Cu GL Ca LFB	4360.040	NaN	2215.778	NaN	26.553	0.083	18.699	0.010	13.514	0.046	9.564	0.0082	-967.74	-888.01	159.47	2.36E-35	0	0
Df Cu GL Ar SB	25003.380	NaN	12923.020	NaN	50.781	0.083	51.246	0.010	26.135	0.043	26.702	0.0076	-1007.50	-927.48	160.05	1.76E-35	0	1
SEF Cu AgL Ar SB	582.612	37169.410	296.914	18945.250	99.154	0.083	154.596	0.010	51.664	0.043	82.496	0.0076	-1052.88	-972.72	160.32	1.53E-35	0	1
SEF Cu GL Ar SB	45828.820	NaN	23298.320	NaN	92.523	0.083	131.766	0.010	46.366	0.043	64.971	0.0076	-1007.47	-927.31	160.34	1.53E-35	0	1
Df Cu AgL Ar SB	60.228	66.231	30.693	33.786	120.106	0.083	189.570	0.010	61.800	0.043	98.647	0.0076	-1053.11	-972.64	160.95	1.12E-35	0	0
SEF Cu AgL Ca LFB	109.423	159.801	55.814	81.539	218.157	0.083	746.165	0.010	112.712	0.046	391.387	0.0082	-1013.21	-932.70	161.04	1.08E-35	0	0
Df Cu AgL Ca LFB	123.081	191.956	62.776	97.925	245.869	0.083	853.243	0.010	125.876	0.046	439.523	0.0082	-1013.20	-932.67	161.04	1.07E-35	0	0

SEF Cu GL Ca LFB	74.515	90.666	38.055	46.355	148.934	0.083	265.310	0.010	76.084	0.046	135.871	0.0082	-967.89	-887.30	161.19	9.96E-36	0	1
SEF Cu GL Ar LFB	14414.070	NaN	7380.067	NaN	26.845	0.077	18.990	0.009	13.690	0.040	9.752	0.0074	-994.70	-907.63	174.14	1.53E-38	0	1
Df Cu GL Ar LFB	56014.280	NaN	27961.370	NaN	99.503	0.077	138.622	0.009	50.866	0.039	71.132	0.0074	-994.78	-907.02	175.52	7.71E-39	0	1
SEF Cu AgL Ar LFB	100.753	141.149	51.360	71.977	201.248	0.077	499.084	0.009	102.988	0.040	256.858	0.0074	-1040.19	-952.31	175.77	6.79E-39	0	1
Df Cu AgL Ar LFB	67.563	78.538	34.440	40.068	135.232	0.077	226.553	0.009	68.415	0.039	113.960	0.0074	-1040.30	-952.34	175.92	6.29E-39	0	1
SEF Cu AgL Bo SB	92.598	128.731	47.125	65.534	186.730	0.122	NaN	0.013	90.740	0.066	NaN	0.0096	-1129.61	-1035.28	188.65	1.08E-41	0	1
SEF Cu GL Bo SB	90.848	125.303	46.278	63.862	180.152	0.122	NaN	0.014	95.142	0.066	NaN	0.0097	-1084.20	-989.78	188.85	9.82E-42	0	0
Df Cu GL Bo SB	124.461	198.337	63.391	101.029	249.354	0.122	995.481	0.014	125.577	0.066	495.426	0.0097	-1084.15	-989.66	188.97	9.23E-42	0	0
Df Cu AgL Bo SB	58.759	67.537	29.903	34.402	117.819	0.122	197.476	0.014	58.839	0.066	96.800	0.0097	-1129.74	-1035.15	189.18	8.32E-42	0	1
Df Cu AgL Bo LFB	154.347	284.572	78.569	144.857	309.061	0.116	1974.550	0.013	156.090	0.062	989.886	0.0093	-1116.76	-1016.61	200.31	3.19E-44	0	1
Df Cu GL Bo LFB	146.441	259.297	74.558	131.940	292.762	0.116	1384.019	0.013	149.061	0.062	704.134	0.0093	-1071.36	-971.19	200.33	3.16E-44	0	1
SEF Cu GL Bo LFB	121.642	191.422	61.973	97.539	243.011	0.116	794.291	0.013	124.154	0.062	406.847	0.0093	-1071.38	-971.20	200.36	3.10E-44	0	0
SEF Cu AgL Bo LFB	87.485	118.888	44.533	60.541	174.246	0.116	408.605	0.013	90.131	0.062	214.815	0.0093	-1116.85	-1016.64	200.41	3.03E-44	0	1

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