Sexual size dimorphism of bark and ambrosia beetles

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Preface

I would like to thank Lawrence Kirkendall for helping me during this semester, and for enthusiastic conversations about the world of beetles and all the other random subjects conversations with him often wander off to.

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Abstract

Size is a defining feature of an animal and is a result of counteracting forces of selection, and studying size and SSD can reveal what drives selection of body size in a given direction. Scolytinae and Platypodinae are diverse groups, representing many different mating systems and feeding strategies, and are for this reason interesting research subjects. The influence of mating systems, initiating sex, feeding type and initiating sex on evolution of size in species of bark and ambrosia beetles was investigated for nine species of ambrosia beetles and twelve species of bark beetles.

Male biased SSD was found in all highly polygynous species of both bark and ambrosia beetles. In mildly polygynous and monogynous species, patterns were more diffuse, but in monogynous bark beetles there appeared to be a trend of female biased SSD. In several male initiated systems, where width of females is restricted, females were shown to evolve longer bodies than males. Ambrosia beetles had much less variation in the traits measured than did bark beetles, possibly caused by either tunneling practices or the more uniform resource quality of ambrosia beetles. Female initiated species of bark beetles were significantly wider than male initiated species, suggesting that male initiation limits evolution of body size.

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Introduction

Size and shape are defining traits of all animals, impacting a variety of basic functions, such as dispersal ability, intraspecific competition and reproductive output (Foelker and Hofstetter, 2014). These functions are in turn selected upon by natural and sexual selection, and thus studying size differences between species and between individuals of a species can reveal a lot about evolutionary pressures acting on that species.

Sexual dimorphism is the result of counteracting sources of selection leading to separate morphological optima in the two sexes (Blanckenhorn, 2000, Butler et al., 2000, Stillwell et al., 2009), and is widespread in animals (Shine, 1989) and in plants (Fairbairn, 1997). Sexual size dimorphism (SSD), a type of sexual dimorphism specifically related to size and shape, may vary greatly between species; from heavily female-biased in the anglerfish where the female can be >20 times longer than the male (Pietsch, 1976), to extremely male-biased in the shell-brooding cichlid where the male has more than 10 times the body weight of the female (Schütz and Taborsky, 2000). Large size has a positive effect on fecundity in females (Shine, 1989, Blanckenhorn, 2005, Stillwell et al., 2009), and female-biased SSD occurs when selection on larger body size for females is stronger than any selection on males to be larger. Male-biased SSD on the other hand is favored in species with strong sexual selection on male-male competition or if females are choosing mates dependent on size (Shine, 1989, Blanckenhorn, 2005, Stillwell et al., 2009).

A biased SSD may also be a result of selection pressure on a sex to be smaller. This can happen under special circumstances, such as high juvenile mortality, high degrees of sperm competition or being in a food-restricted environment (Blanckenhorn, 2005). The latter one is the case in anglerfish, dwarfed males have smaller energy requirements and can therefore search longer for females.

Size is a result of many underlying factors, and proximate factors such as growth rates, energy requirements etc. can inhibit a sex from reaching its theoretical size optimum. Determining which factors influence size in a given species and their relative importance is often difficult, though in females reproduction has been shown to be such a factor (Bonnet et al., 2011).

The groups of species studied in this thesis are Scolytinae and Platypodinae, subfamilies of weevils which live most of their lives inside dead wood or other plant tissue (Kirkendall et al., 2015). There are about 6000 species of Scolytidae and about 1400 species of Platypodidae globally, and though bark and ambrosia beetles are known for their ability to kill live trees, this is not widespread as less than 1% of bark beetles are estimated to regularly kill live trees (Kirkendall et al., 2015).

Scolytinae and Platypodinae are grouped together in this study as they are very similar in morphology and ecology and have traditionally been studied together, though in later years it has been discovered that they may not be closely related (Kirkendall et al., 2015). Bark beetles are beetles that feed on plant tissue, which can vary a great deal in nutritional quality, while ambrosia beetles feed on fungus they carry with them and cultivate in their tunnels and is thought to be more uniform in quality (Kirkendall, 1983). SSD in bark and ambrosia beetles, as in insects, is generally female biased (Fairbairn, 2013).

The ancestral mating system of bark and ambrosia beetles is thought to be female initiated monogyny (Kirkendall et al., 2015), but bark and ambrosia beetles employ a wide range of mating strategies; including strict monogyny, harem polygyny and inbreeding. Reversal of sex roles has evolved in some monogynous species of bark and ambrosia beetles, likely resulting from male initiated polygynous species reverting back to monogyny (Kirkendall, 1983). In all polygynous species of Scolytinae and Platypodinae males initiate galleries.

In female initiated species the female constructs the tunnel system alone. In species where the male initiates tunneling, the male only tunnels a short distance before he is courted by a female who later completes the tunnel system. Parental care is widespread in bark and ambrosia beetles, and the male both helps by blocking the tunnel entrance, preventing predators from entering the gallery, and maintaining the gallery by expelling frass, a mixture of wood and excrement (Kirkendall, 1983).

The operational sex ratio (OSR) for any given species impacts the strength of selection on sexes in that species. If there are many males for each fertile female, then selection pressure on males increase, as the cost of not achieving mates are huge. This may result in guarding behavior, or if female biased OSR occurs, roaming (Kirkendall, 1983). OSR in bark beetles will likely change over time, as the initial OSR should be close to 1 (at least in outbreeding species), but as flying or searching for new host material, it will likely change. The initiating sex has to locate the specific

breeding resource, which may be rare, find a suitable spot on the bark and construct the tunnel. A lot of risk is associated with this; not finding the required breeding resource eliminates chances of mating, predators are can easily prey on beetles when they are not ensconced in wood, and if attacking live trees the beetles may be killed by host defenses (Kirkendall et al., 2015). The sex that courts has in many species the advantage that the initiating sex emits pheromones to help conspecifics locate their breeding site (Vité and Francke, 1976). Coupled with the fact that mating in many species occurs inside the gallery system, OSR in many bark and ambrosia beetles is likely to be biased towards the courting sex, and selection pressure might be stronger in the courting sex.

Tunnels are not likely to be made much wider than the initiating sex as the narrowness of the tunnel protects the beetles from the environment and predators. In one species the relationship between the initiating sex's width and the courting sex's width was studied, revealing that *Dendroctonus ponderosae* Hopkins males more than 10% larger than the female could enter the female gallery, but smaller males were more likely to enter than large ones (Reid and Baruch, 2010). This indicates that width of the initiating sex is not a strong limitation on the width of the courting sex in this species, though it must be noted that this is a very large species, average of 5.5 mm long (Wood, 1982), and larger beetles may need more room to move as they could be less agile.

When assessing size of bark and ambrosia beetles, pronotum width or total length are the traits most often measured (Wood, 1982, Teale et al., 1994, Reid and Roitberg, 1995, Lindeman and Yack, 2015). Which trait is measured can have a major influence on the estimate of SSD in a species (Stillwell et al., 2009), and measuring several characteristics of a species could minimize such bias.

Studies of Scolytidae and Platypodidae have the potential to answer many questions related to the evolution of size and shape, as a great variety of mating systems and feeding types are represented in these two groups. Investigating sexual size dimorphism of animals in relation to mating systems has been done in birds (Raihani et al., 2006, Székely et al., 2000) and in fish (Walker and McCormick, 2009), but not in bark beetles. Generally, in arthropods, females are the larger of the sexes, but there are exceptions to this rule. I hypothesize that mating system, initiating sex and feeding type can explain patterns of SSD in bark and ambrosia beetles. The tunnel systems bark and ambrosia beetles construct are somewhat different in the two groups (Kirkendall, 1983). In ambrosia beetles, the tunnel adult(s) construct and use to enter and exit the gallery, is the same

which the offspring exits through once mature. This might introduce a limitation on the maximum width of offspring attempting to exit the gallery. In bark beetles, each larvae digs its own separate tunnel out from the gallery, and its width is therefore not limited in the same way. I hypothesize that tunnel width imposes limitations on width. From these two hypotheses, several predictions can be made. I predict that males will be the wider sex in polygynous species, as larger males have been shown to have higher mating success that smaller ones (Reid and Roitberg, 1995), and that in monogynous species females should be the wider sex, as is the norm in insects. In male initiated species of bark and ambrosia beetles, I predict that females will become longer than conspecific males if selection pressure on size is strong enough. Ambrosia beetles use a single tunnel to enter and exit the gallery, and maximum width of offspring will be restricted. As a result of this, I predict that variation in width in ambrosia beetles will be lower than in bark beetles. Additionally, I predict that female initiated species of bark and ambrosia beetles will be wider than male initiated species, as females in male initiated species are limited in width by the tunnel started by males.

Materials and methods

The Scolytinae and Platypodinae specimens measured were acquired from the "Naturhistorische Museum Wien" (the Karl E. Schedl collection), University Museum of Bergen, and Lawrence Kirkendall's collection (Dept. Biology, University of Bergen). 12 species of bark beetles and 9 species of ambrosia beetles were measured, a total of 902 beetles.

All individuals were photographed using a Leica Z16 APO A (Type DFC295) trinocular stereomicroscope connected to a Windows XP computer (service pack 3) and LAS V3.6.0 build 488 (Leica Application Suite). The software was calibrated using a Carl Zeiss 1 mm 100/100mm glass slide. Pinned bark beetles were positioned ventral side down, horizontally, to minimize measuring error caused by angled photos. In cases where parts of a beetle's body were unavoidably angled, two pictures were taken of the pronotum and elytra instead of one.

Measuring was done digitally, using the pictures taken by the microscope's camera and Leica Application Suite (LAS), measuring to the closest µm. Two of the measuring tools provided by LAS were used, a three-point line measure (Figure 1a) and a two-point line measure (Figure 1b). Length of elytra was measured from the most anterior part of the elytra to the most posterior point of the elytra (Figure 1a), using a three-point line tool. Pronotum and elytra width were measured using two-point line tool, finding the distance between two points on the widest part of the pronotum (Figure 1c). To accurately determine width, several measures on both elytra and pronotum were sometimes taken to find the widest measure (Figure 1b). Pronotum length was measured using either the two-point line tool, if the most posterior part of pronotum was at the center of the posterior part of the pronotum (Figure 1b), or three-point line tool, where two points (the posterior-most points of the pronotum) (Figure 1a) on the posterior end and one on the anterior end were used to measure. When pictures were unclear, specimens were viewed using only the microscope to aid in measuring and thus increase accuracy.

All results were recorded in an excel workbook in µm to increase efficiency and minimize error, as the use of commas was not needed. Individuals not already sexed were sexed with help from Lawrence Kirkendall. Sex, length and width of elytra and pronotum, pin number, mating system, initiating sex and where individuals had been collected was included in the workbook. Species were allocated into one of three categories, dependent on if males were known to mate with one

female (monogynous), usually just one or two females (mild polygynous) or where mating with three or more females is common (polygynous).

To assess measuring error, 8 individuals of the first species measured, *D. mesoamericanus*, were measured thrice. Measuring error ranged from 0 to 3% with a single outlier of 6%, with a mean of 1.3%. This number is likely exaggerated as this was at the start of the measuring process.

All analyses were performed using RStudio (version 0.99.896). T-tests and linear models were used to test hypotheses.
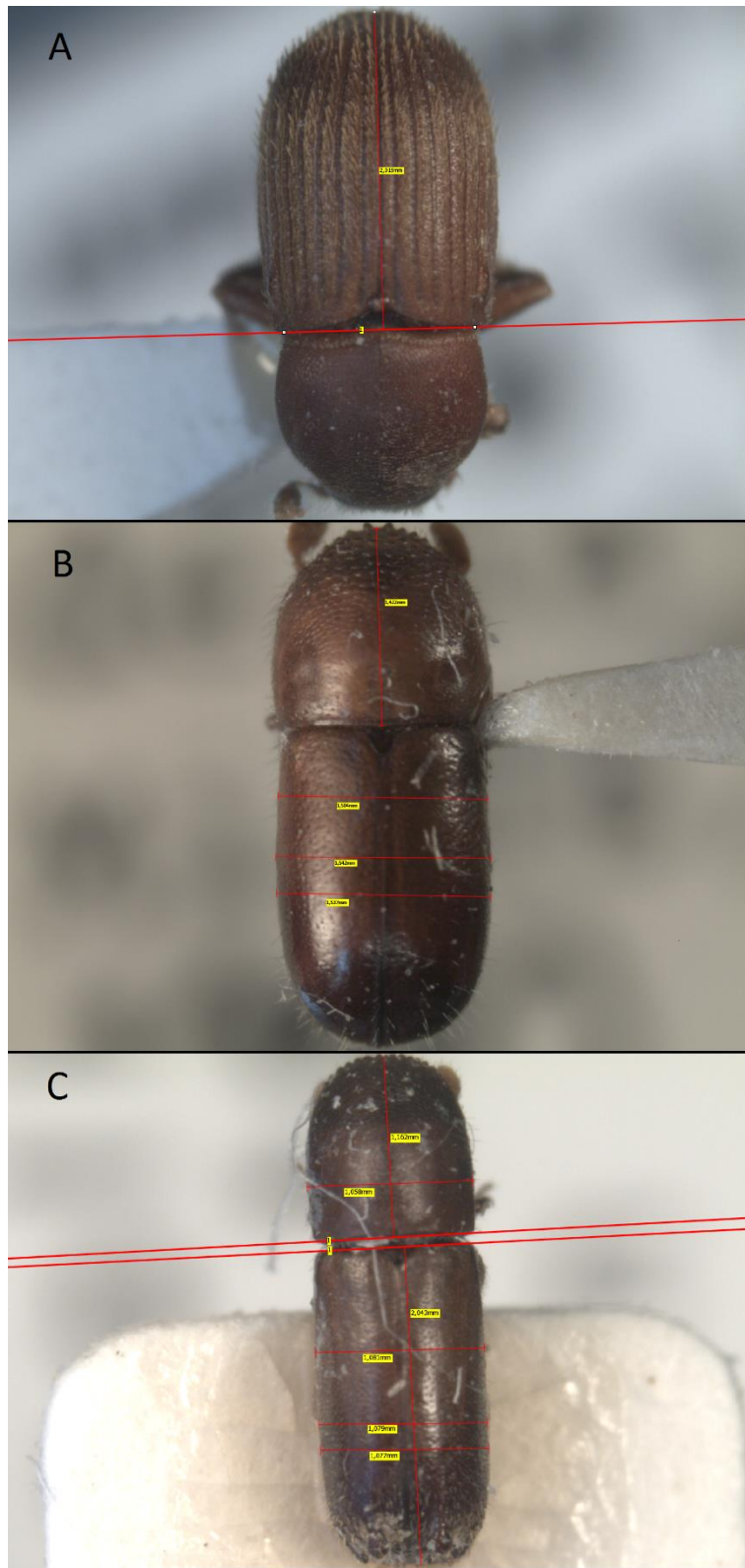
Figure 1: Examples of measuring tools and use, measures are in µm. a) Three-point line tool measure of elytra length, b) two-point line tool measure of pronotum length and of elytra width, three for accuracy, c) example of a fully measured beetle

Results

The ratio of mean male to female elytra width in bark beetles was significantly different between polygynous species and monogynous species (p=<0.001), but not between monogynous and polygynous species (p=0.19) or between polygynous and mild polygynous species (p=0.11) (Figure 2). Males were consistently wider than females in polygynous species, narrower than females in monogynous species and close to the same width as females in mild polygynous species. For ambrosia beetles the same pattern held for polygynous species, but monogynous species were highly variable (0.96-1.05), and the mild polygynous species had larger females than males (Figure 3).

Plotting elytra length/elytra width for both sexes showed that in ambrosia beetles, the sexes of one species did not overlap in its 95% CI, *G. pustulatus*. This species is male-initiated and bigynous, and it is the female is comparatively longer (Figure 4). In bark beetles, four species did not overlap in their 95% CI: *P. bidentatus, P. poligraphus, S. atratus* and *S. glabrellus*. All four are male-initiated species, two are monogynous and two are polygynous, and in all four females were the comparatively longer sex (Figure 5).

Ambrosia beetles were much less variable in size than bark beetles (Table 1). Mean elytra width CV was 8% for bark beetles and 4% for ambrosia beetles. The coefficient of variance (CV) was significantly different between ambrosia beetles and bark beetles for elytra width (p<0.001), elytra length (p<0.001), pronotum width (p<0.001) and pronotum length (p=0.0015). Inter-sexual differences in bark beetles were not significantly different from intersexual differences in ambrosia beetles (p=0.37). Length of pronotum and elytra were the most variable traits: an average of 5% in ambrosia beetles and 9% in bark beetles for pronotum, 5% in ambrosia beetles and 8% in bark beetles for elytra. Width showed the same pattern, with pronotum width and elytra width CV for ambrosia beetles being 3% and 4%, respectively, and 7% CV for both measures of bark beetles.

Female-initiating species of bark beetles were significantly wider (group mean 1.64 mm) than male-initiated species (group mean 1.02 mm) (p<0.001) (Figure 6). There was no such pattern for ambrosia beetles (Figure 7). Pronotum width and elytra width were found to be highly correlated (0.9797866). Elytra width and elytra length were found to be somewhat correlated (0.8430306).

Figure 2: Mean female elytra width / male elytra width, mating system and initiating sex for bark beetles. Species are indicated by a circle or triangle, x marks species where mating system or initiating sex is not certain Points are scattered horizontally for readability.
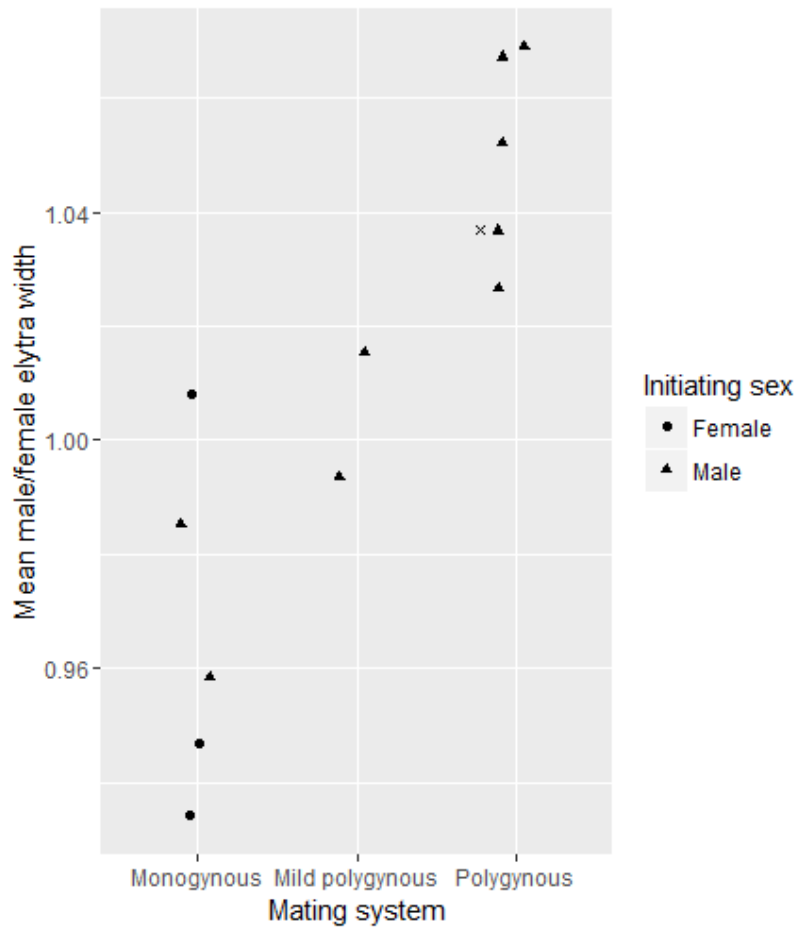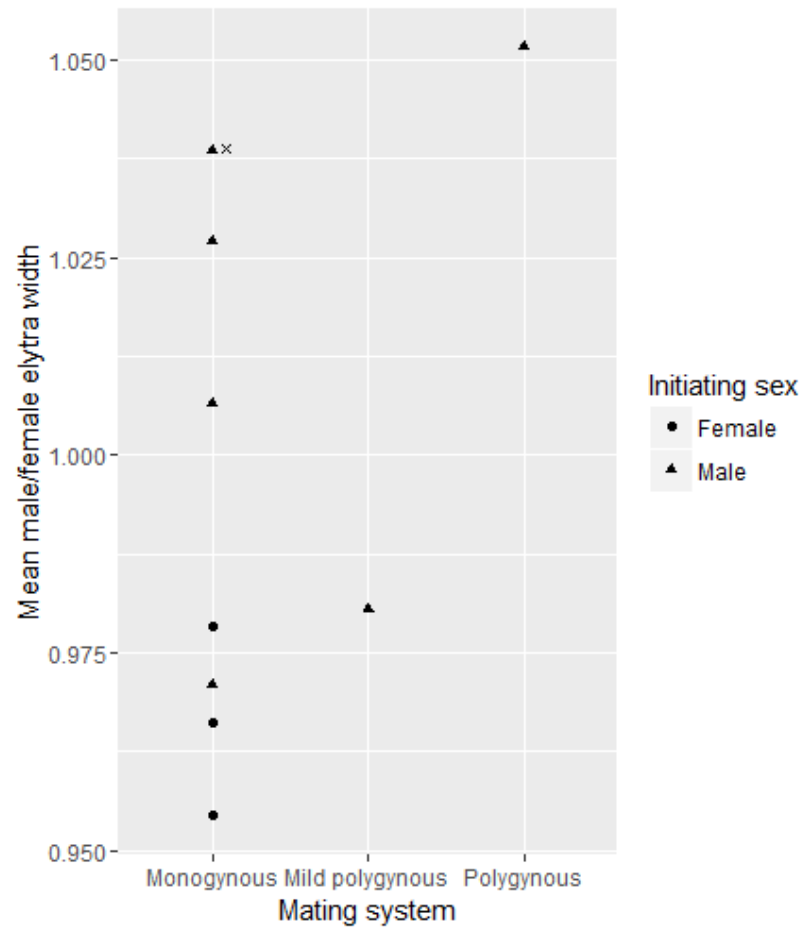
Figure 3: Mean female elytra width / male elytra width, mating system and initiating sex for ambrosia beetles. Species are indicated by a circle or a triangle. X marks species where mating system or initiating sex is uncertain.

Figure 4: Elytra length/elytra width for bark beetles. Triangles and circles give the means and the error bars are 95% CI of the the mean.

Figure 5: Elytra length/elytra width for ambrosia beetles Triangles and circles give the means and the error bars are 95% CI of the mean.

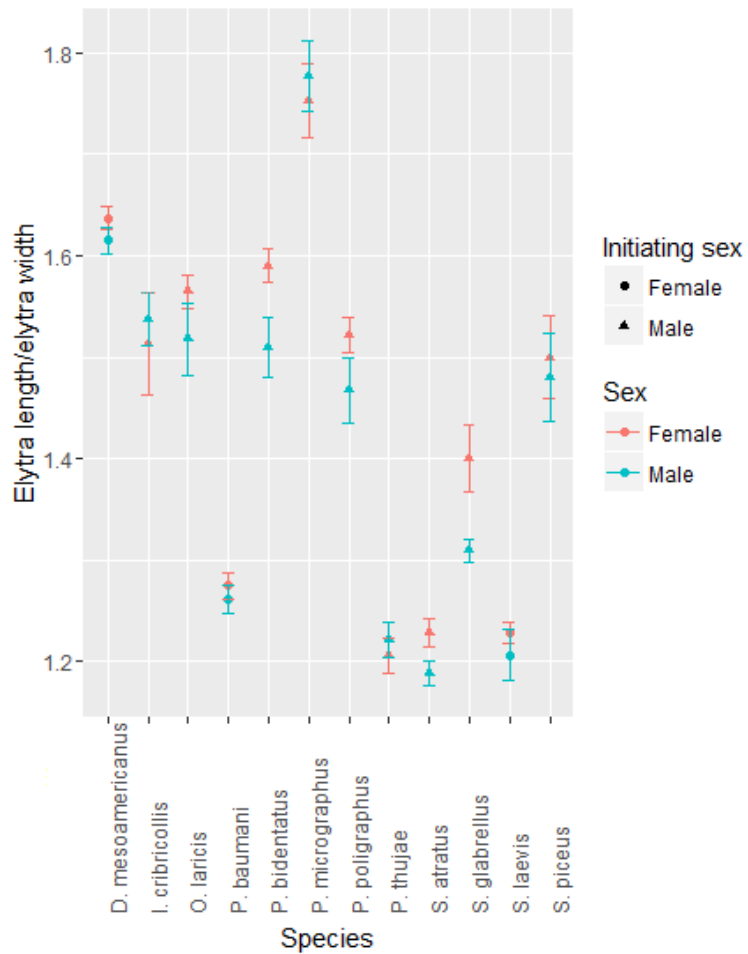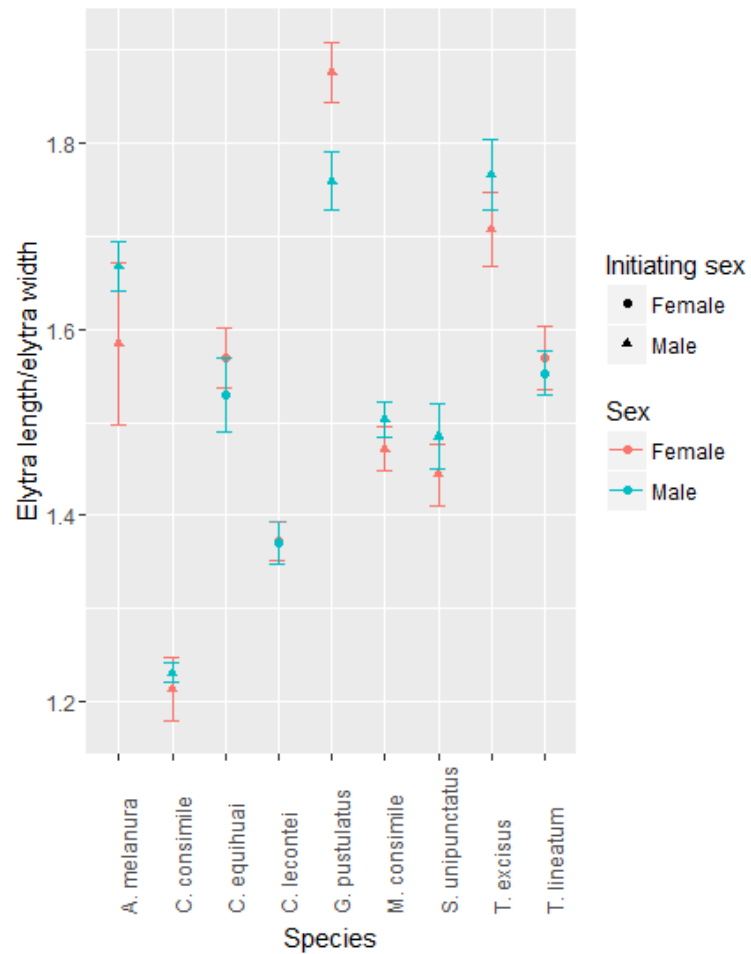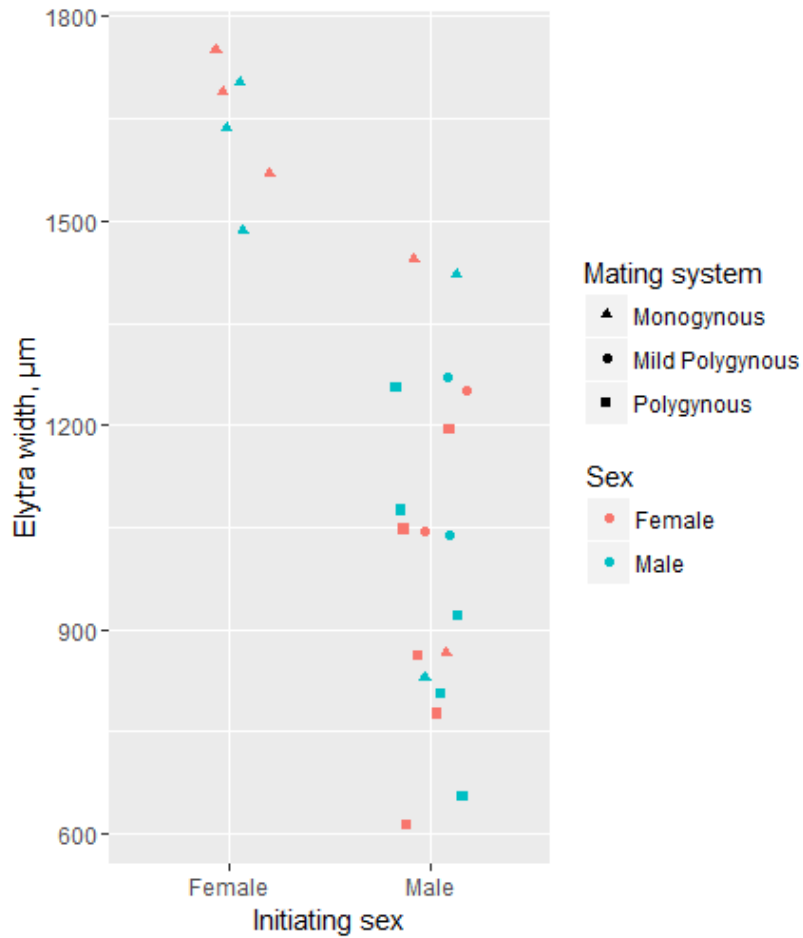Figure 6: Elytra width, mating system and initiating sex plots for bark beetles. Points are scattered horizontally for readability.
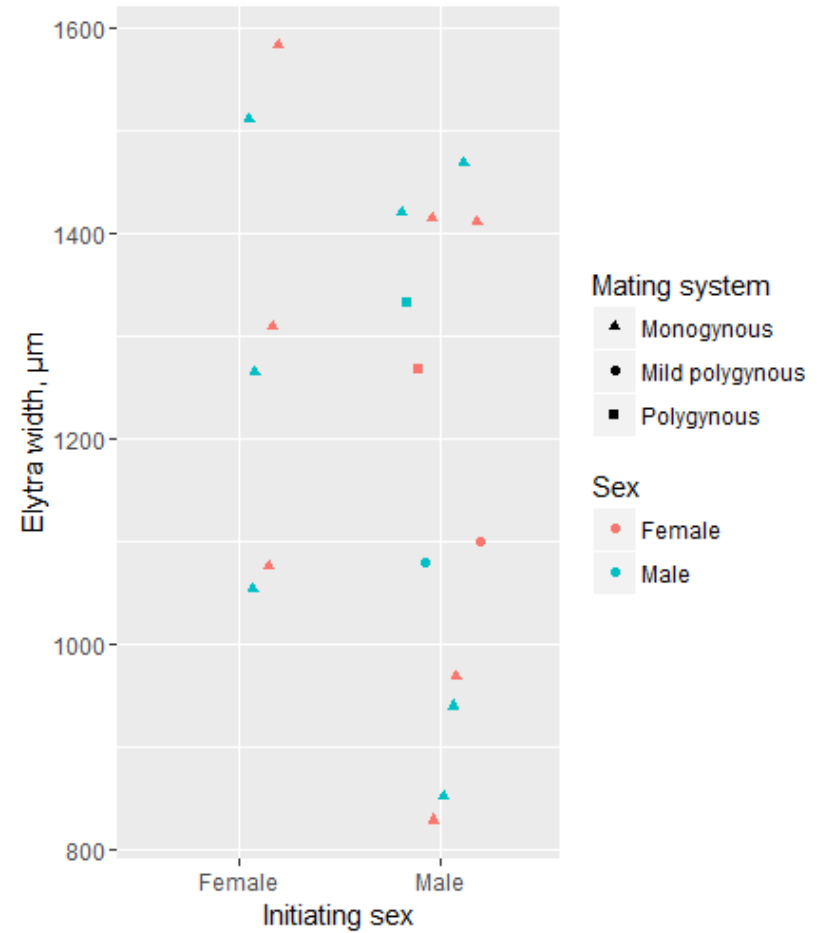

Figure 7: Elytra width, mating system and initiating sex plots for ambrosia beetles. Points are scattered horizontally for readability.

Table 1: Averages, minimum- and maximum values, standard deviation and CV for species measured. Pronotum and elytra are abbreviated pn and ey, espectively. l=length, w=width. * indicates species where the given mating system or initiating sex is not certain, but estimated based on ecology and phylogeny.

Group	Species	Init. sex	Mating system	n Sex	apnl	minpnl	maxpnl	stdevpnl	cvpnl	apnw	minpnw	maxpnw	stdevpnw	cvpnw	aeyl	mineyl	maxeyl	stdeveyl	cveyl	aeyw	mineyw	maxeyw	stdeveyw	cveyw
Ambrosia beetles	Amphicranus melanura (Blandford)	M	Monogynous*	7 M	1,92	1,81	2,02	0,07	4%	1,44	1,36	1,48	0,04	3%	2,44	2,27	2,54	0,10	4%	1,47	1,38	1,51	0,04	3%
	A. melanura (Blandford)	M	Monogynous*	5 F	1,85	1,84	1,87	0,01	1%	1,40	1,37	1,43	0,02	2%	2,32	2,29	2,36	0,04	2%	1,44	1,41	1,47	0,03	2%
	Coorthylus consimilis Wood	M	Monogynous	36 M	1,32	1,22	1,46	0,05	4%	1,43	1,34	1,34	0,04	3%	1,75	1,61	1,90	0,06	4%	1,42	1,35	1,50	0,04	3%
	C. consimilis Wood	M	Monogynous	14 F	1,26	1,16	1,36	0,05	4%	1,39	1,31	1,31	0,03	2%	1,72	1,55	1,94	0,09	5%	1,41	1,32	1,47	0,04	3%
	Cnesinus lecontei Blandford	F	Monogynous	8 M	1,01	0,93	1,09	0,05	5%	1,30	1,17	1,36	0,07	5%	2,07	1,81	2,22	0,12	6%	1,51	1,34	1,58	0,07	5%
	C. lecontei Blandford	F	Monogynous	11 F	1,12	1,04	1,19	0,05	4%	1,37	1,31	1,44	0,05	3%	2,17	1,99	2,36	0,11	5%	1,58	1,47	1,72	0,07	4%
	C. equihuai Wood	F	Monogynous	7 M	0,79	0,64	0,86	0,08	10%	0,90	0,76	0,98	0,07	8%	1,61	1,33	1,75	0,13	8%	1,05	0,90	1,12	0,08	8%
	C. equihuai Wood	F	Monogynous	12 F	0,84	0,72	0,91	0,06	7%	0,90	0,80	0,96	0,04	5%	1,69	1,47	1,83	0,09	6%	1,08	0,97	1,14	0,04	4%
	Gnathotrupes pustulatus Schedl	M	Monogynous	30 M	1,19	1,07	1,32	0,07	6%	1,05	0,96	1,11	0,03	3%	1,90	1,66	2,18	0,12	6%	1,08	0,98	1,17	0,04	4%
	G. pustulatus Schedl	M	Monogynous	33 M	1,27	1,16	1,38	0,05	4%	1,06	1,00	1,20	0,05	4%	2,06	1,82	2,37	0,12	6%	1,10	1,01	1,20	0,04	4%
	Monarthrum consimile (Blandford)	M	Polygynous	18 M	1,44	1,36	1,56	0,05	3%	1,30	1,24	1,35	0,03	3%	2,00	1,82	2,10	0,08	4%	1,33	1,24	1,41	0,04	3%
	M. consimile (Blandford)	M	Polygynous	8 F	1,44	1,27	1,54	0,10	7%	1,24	1,20	1,29	0,03	3%	1,86	1,70	1,97	0,10	5%	1,27	1,19	1,32	0,05	4%
	Scolytodes unipunctatus (Blandford)	M	Monogynous	11 M	0,91	0,85	0,99	0,04	4%	0,91	0,88	0,92	0,01	1%	1,39	1,34	1,46	0,04	3%	0,94	0,90	0,99	0,03	3%
	S. unipunctatus (Blandford)	M	Monogynous	10 F	0,94	0,89	0,99	0,04	4%	0,93	0,92	0,94	0,01	1%	1,40	1,33	1,45	0,04	3%	0,97	0,94	1,01	0,02	2%
	Teloplatypus excisus (Chapuis)	M	Monogynous	12 M	0,82	0,77	0,86	0,02	3%	0,81	0,77	0,84	0,02	2%	1,50	1,45	1,61	0,05	3%	0,85	0,82	0,91	0,03	4%
	T. excisus (Chapuis)	M	Monogynous	4 F	0,78	0,76	0,79	0,01	2%	0,79	0,78	0,81	0,01	1%	1,41	1,37	1,43	0,03	2%	0,83	0,81	0,85	0,02	2%
	Trypodendron lineatum (Olivier)	F	Monogynous	33 M	0,92	0,77	1,11	0,07	7%	1,24	1,11	1,34	0,05	4%	1,96	1,71	2,21	0,12	6%	1,26	1,13	1,37	0,06	4%
	T. lineatum (Olivier)	F	Monogynous	19 F	1,11	1,01	1,21	0,06	5%	1,31	1,23	1,40	0,04	3%	2,05	1,79	2,21	0,12	6%	1,31	1,21	1,38	0,06	4%
Bark beetles	Dendroctonus mesoamericanus Armendáriz-Toledano & Sullivan	F	Monogynous	30 M	0,94	0,78	1,11	0,09	9%	1,47	1,24	1,66	0,12	8%	2,40	2,01	2,77	0,18	8%	1,49	1,24	1,71	0,12	8%
	D. mesoamericanus Armendáriz-Toledano & Sullivan	F	Monogynous	30 F	1,02	0,86	1,12	0,07	7%	1,55	1,37	1,71	0,09	6%	2,57	2,23	2,79	0,15	6%	1,57	1,40	1,74	0,09	6%
	Ips cribricollis (Schedl)	M	Polygynous	10 M	1,46	1,23	1,78	0,12	8%	1,25	1,01	1,54	0,11	9%	1,93	1,58	2,31	0,16	8%	1,26	1,06	1,52	0,10	8%
	I. cribricollis (Schedl)	M	Polygynous	8 F	1,40	1,23	1,52	0,10	7%	1,19	1,11	1,23	0,04	3%	1,80	1,67	1,88	0,07	4%	1,19	1,15	1,25	0,04	3%
	Orthotomicus laricis (Fabricius)	M	Mild polygynous	9 M	1,37	1,24	1,52	0,09	7%	1,23	1,13	1,31	0,07	5%	1,93	1,74	2,14	0,11	6%	1,27	1,18	1,34	0,05	4%
	O. laricis (Fabricius)	M	Mild polygynous	28 F	1,32	1,20	1,32	0,07	5%	1,20	1,10	1,34	0,06	5%	1,96	1,73	2,19	0,12	6%	1,25	1,14	1,39	0,06	5%
	Phloesinus baumani Hopkins	F	Monogynous	27 M	1,13	0,80	1,48	0,13	12%	1,51	1,01	1,82	0,15	10%	2,06	1,28	2,45	0,22	11%	1,64	1,07	1,91	0,16	10%
	P. baumani Hopkins	F	Monogynous	42 F	1,26	1,02	1,55	0,15	12%	1,65	1,43	1,94	0,13	8%	2,23	1,90	2,59	0,18	8%	1,75	1,54	2,00	0,12	7%
	P. thujae (Perris)	M	Mild polygynous	40 M	0,73	0,58	0,87	0,06	8%	0,96	0,83	1,11	0,06	6%	1,27	1,09	1,40	0,08	7%	1,04	0,89	1,15	0,07	7%
	P. thujae (Perris)	M	Mild polygynous	44 F	0,69	0,54	0,85	0,07	10%	0,94	0,81	1,09	0,07	8%	1,26	0,99	1,53	0,12	10%	1,04	0,88	1,19	0,08	7%
	Pityogenes bidentatus (Herbst)	M	Polygynous	16 M	0,97	0,83	1,06	0,06	6%	0,90	0,76	0,97	0,05	5%	1,39	1,12	1,53	0,09	7%	0,92	0,79	1,00	0,05	5%
	P. bidentatus (Herbst)	M	Polygynous	26 F	0,91	0,74	1,05	0,09	10%	0,82	0,69	0,94	0,07	9%	1,37	1,14	1,56	0,13	9%	0,86	0,73	0,97	0,07	8%
	Pityophterus micrographus (Linnaeus)	M	Polygynous	12 M	0,65	0,52	0,82	0,09	13%	0,63	0,53	0,85	0,09	14%	1,16	1,01	1,55	0,16	14%	0,65	0,57	0,89	0,09	14%
	P. micrographus (Linnaeus)	M	Polygynous	18 F	0,63	0,54	0,74	0,06	9%	0,58	0,51	0,69	0,05	9%	1,07	0,87	1,26	0,10	10%	0,61	0,54	0,71	0,05	8%
	Polygraphus poligraphus (Linnaeus)	M	Polygynous	22 M	0,76	0,58	0,92	0,08	11%	1,02	0,81	1,20	0,10	10%	1,58	1,31	1,84	0,17	11%	1,07	0,88	1,22	0,11	10%
	P. poligraphus (Linnaeus)	M	Polygynous	51 F	0,72	0,55	0,91	0,09	12%	0,96	0,75	1,15	0,10	10%	1,59	1,27	1,95	0,17	11%	1,05	0,84	1,24	0,11	10%
	Scolytodes atratus (Blandford)	M	Monogynous	41 M	1,25	0,94	1,46	0,13	10%	1,28	1,08	1,47	0,10	8%	1,69	1,46	1,99	0,14	9%	1,42	1,20	1,63	0,11	8%
	S. atratus (Blandford)	M	Monogynous	35 F	1,17	1,01	1,42	0,10	9%	1,27	1,11	1,45	0,09	7%	1,77	1,44	2,14	0,17	10%	1,44	1,23	1,64	0,11	7%
	S. glabrellus Wood & Bright	M*	Polygynous*	36 M	0,82	0,66	0,94	0,07	8%	0,77	0,64	0,87	0,05	7%	1,05	0,89	1,18	0,06	6%	0,80	0,67	0,91	0,05	6%
	S. glabrellus Wood & Bright	M*	Polygynous*	19 F	0,76	0,60	0,96	0,08	11%	0,74	0,63	0,84	0,04	6%	1,09	0,93	1,15	0,06	5%	0,78	0,67	0,85	0,05	6%
	S. piceus (Blandford)	M	Monogynous	20 M	0,68	0,62	0,75	0,04	5%	0,71	0,61	0,77	0,04	5%	1,22	1,14	1,36	0,07	5%	0,83	0,68	0,96	0,07	8%
	S. piceus (Blandford)	M	Monogynous	32 F	0,72	0,60	0,81	0,05	7%	0,74	0,63	0,82	0,04	6%	1,29	1,14	1,41	0,06	5%	0,87	0,74	1,01	0,07	8%
	Scolytus laevis Chapuis	F	Monogynous	8 M	1,55	1,36	1,71	0,11	7%	1,68	1,51	1,84	0,11	6%	2,05	1,81	2,21	0,14	7%	1,70	1,52	1,85	0,11	7%
	S. laevis Chapuis	F	Monogynous	11 F	1,54	1,39	1,82	0,12	8%	1,66	1,53	1,89	0,10	6%	2,07	1,90	2,40	0,13	6%	1,69	1,55	1,97	0,11	6%

Discussion

Results were consistent with both hypotheses; mating system, initiating sex and feeding type can explain patterns of SSD, and tunnel width imposes limitations on width.

In polygynous species of bark and ambrosia beetles, males were the wider sex, while mildly polygynous species showed no clear trend towards either sex being widest (Figure 2, 3). This indicates that in strongly polygynous species there is strong selection for males to be larger than females, and supports the prediction that SSD will be male biased, but only in highly polygynous species. Selection pressure on larger size on males of mildly polygynous species is apparently not strong enough to reverse SSD. If fighting amongst males is widespread, and larger males are more successful in these bouts, males could evolve to be larger than females and help explain these findings, though no information on fighting has been found regarding the polygynous species measured. Large individuals of the polygynous bark beetle *Ips pini* (Say) have been shown to have higher mating success than smaller males, apparently due to increased parental investment, and additional mating opportunities (Reid and Roitberg, 1995). Increased reproductive output could be the cause of the size difference seen in polygynous bark and ambrosia beetles, though data is not available for the species measured to support this hypothesis. It is entirely possible that advantages to being small in polygynous species could help explain why males are larger than females. Smaller offspring have lesser energy requirements, and a female can lay a higher number of eggs per unit of resource. Polygynous species often have several females in each gallery, limiting available resource per female, and if the cost of offspring being small is not too great, then smaller offspring can evolve. Selection for smaller offspring would ultimately end in smaller adults, and thus for the observed patterns to occur, selection on larger males would have to be strong.

Males and females in monogynous species of bark beetles were either similar in width or females were wider, which somewhat fits my prediction that females should be wider in monogynous species. In bark beetles, there appears to be a trend of females being wider than males, which holds for both male initiated and female initiated species. Male initiated monogyny is a derived trait, and that both male and female initiated monogynous species show the same trend suggests that monogyny selects towards females being wider than males. Females are generally larger than males in insects, and if there is no strong selection pressure for larger males, it is reasonable to expect

females to be the larger sex in bark and ambrosia beetles. Prevalence of fighting is not known for many monogynous species, and if the monogynous bark beetles measured do not exhibit fighting behavior, species that do fight might deviate from the pattern seen. In ambrosia beetles, monogynous species are distributed fairly equally over or under 1 (Figure 3), which does not fit my prediction that monogynous species should have female-biased SSD. It is possible that benefits of being large are not as strong in ambrosia beetles as in bark beetles, due to the more uniform feeding resource of ambrosia beetles possibly increasing fecundity regardless of size. Fighting is known to occur in one monogynous ambrosia beetle, *T. lineatum* (Hadorn, 1933, Fockler and Borden, 1972)*, which will favor larger males, even though for this species, females are still the larger sex.

One species of ambrosia beetle and four species of bark beetles, all male initiated, had significantly longer females than males, indicated by the non-overlap of 95% CI (Figure 4, 5), supporting the hypothesis that tunnel width imposes limitations on female body size. Two of the species are monogynous and three of the species are polygynous, indicating that mating system is not linked to this trend. This suggests that in male initiated species, there is a limitation to width, and selection towards larger size in females results in females growing longer. This result contradicts the fact that in the bark beetle *D. ponderosae* males more than 10% larger than females could enter females' galleries. At 5.5 mm long, this species is larger than any of the ones measured (Table 1), and large beetles may require additional room to move around, and thus construct a wider tunnel relative to themselves compared to smaller beetles. These result suggest that there are factors not covered in this analysis which influence which male initiated species evolve longer females than males, one of which could be OSR. If OSR is highly male-biased, then selection will be stronger on the courting sex. If males choose which females to mate with, and choice is based on size, then selection will favor longer females.

Female initiated species of bark beetles were significantly wider than male initiated species (Figure 6), which supports my hypothesis that tunnel width imposes limitations on body size. This trend is all but missing in ambrosia beetles, though both minimum values and maximum values were higher for female initiated species than male initiated (Figure 7). Data from Wood (1982) reveals that in North and Central American species, the trend is the same for bark beetles: female initiated species tend to be larger than male initiated, but female initiated species are also larger in ambrosia beetles

(Table 2. These discrepancies between my limited data and Wood's can be expected, and it is likely that if more species had been measured, the pattern seen in Wood would be evident in this thesis as well.

Table 2: Means of median length of initiating sexes in bark and ambrosia beetles of North and Central America, data taken from Wood (1982).

BARK BEETLES	N	Average
Female	76	2.3 mm
Male	110	1.8 mm
AMBROSIA BEETLES		
Female	9	3.2 mm
Male	150	2.5 mm

Ambrosia beetles had significantly lower CV than bark beetles, supporting the hypothesis that tunnel width imposes limitations on body size. In addition to tunneling practices of the two groups, this difference could also be caused by the uniform resource quality of fungus as opposed to plant material, which can be highly variable in quality. This may also be the cause of the low number of highly polygynous ambrosia beetles as it is difficult to monopolize good resources, which is thought to be a major driver for polygyny in bark beetles (Kirkendall, 1983).

This thesis is based on work done over four months, from February to June, and the number of species and individuals included in it is therefore limited. This may have resulted in patterns and trends not being revealed, or the appearance of trends that are not actual. The latter is exemplified in the apparent trend that width of ambrosia beetles do not differ between male and female initiated species (Figure 7), which is refuted by Wood's measurements (Table 2). Selection of species may also be a source of error, as even though an attempt was made to include a broad selection of species, species were selected on availability. Measuring error and wrongful sexing of individuals are also sources of error. Additionally, most species are represented by only a single population, and so inter-population differences within a species may obscure results.

As for further research, it would shine new light on the conclusions drawn here if the relationship between beetle width and tunnel width had been elucidated, perhaps through an experimental

approach. Additional statistical analyses could also be applied to this data, such as linear mixed-effects models, as time restricted which analyses could be performed.

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Appendix

R script syntax

```
library("ggplot2")
library("plyr")


# Setter mappe
setwd("C:\\users\\andreas\\desktop\\bark\\")


#Importerer fil
data.df <- read.table("reworkeddata.csv", sep=";", dec=",", header=T)
#legger inn ratios, ell/elw
data.df$rat <- data.df$ell/data.df$elw
#Sjekker om alt er importert riktig
head(data.df)


#lager nytt datasett med gjennomsnitt for alle arter
summarystats.main <- ddply(data.df, .(species,sex,mating_system,initiating_sex,feeding_type),function(x){
  cm <- colMeans(x[, c("ell","elw","pnl","pnw","rat")],na.rm = TRUE)
  data.frame(as.list(cm))
})
summarystats.main


#plotter
ggplot(summarystats.main,aes(x=mating_system,y=elw,colour=sex,
shape=initiating_sex))+geom_jitter(height=0,width=.5)+labs(x="Mating system", y="Elytra width, µm",title="Summary plot")


#plotter for ell/elw ratios
ggplot(summarystats.main,aes(x=mating_system,y=rat,colour=sex,
shape=initiating_sex))+geom_jitter(height=0,width=.5)+labs(x="Species", y="Ratio elL/elW",title="Summary elytra ratios")

ggplot(summarystats.main,aes(x=initiating_sex,y=rat,colour=sex,
shape=initiating_sex))+geom_jitter(height=0,width=.5)+labs(x="Species", y="Ratio elL/elW",title="Summary elytra ratios")


#Lager nye dataset, am=ambrosia, bark=barkbeetle
am.df <- subset(data.df, feeding_type == "ambrosia")
```

```
head(am.df)


bark.df <- subset(data.df, feeding_type == "barkbeetle")

head(bark.df)


#plotter pnw mellom kjønn i AMBROSIA, boxplot

boxplot(am.df$pnw~am.df$sex, main="Ambrosia boxplot", xlab="Sex",ylab="Pronotum width, µm")


#Plotting, aes=aesthetics, facetwrap gjør at alle "species" får eget vindu

plot1 <- ggplot(am.df, aes(x=sex,y=pnw)) +geom_boxplot()+facet_wrap(~species)+labs(title="Ambrosia species")

plot1


#plotter annerledes,labs(labels)axes

ggplot(am.df, aes(x=pnl,y=pnw, colour = sex))+

  geom_point()+facet_wrap(~species) +

  labs(x="Pronotum length, µm",y="Pronotum width, µm", colour="Sex", title="Ambrosia")


#Calculating means dataframe-dataframe plyfunction. colMeans tar gjennomsnitt av de gitte kolonnene

summarystats.am <- ddply(am.df, .(species,sex,mating_system,initiating_sex,feeding_type),function(x){

  x <- x[, c("ell","elw","pnl","pnw", "rat")]

  cm <- colMeans(x, na.rm = TRUE)

  sds <- colwise(sd)(x, na.rm = TRUE)

  cv <- sds / cm

  data.frame(as.list(c(cm, cv)))

})

#Plotter pnw, jitter gjør at punktene flytter seg litt fra der de er

ggplot(summarystats.am,aes(x=initiating_sex,y=pnw,colour=sex, shape = mating_system)) + geom_jitter(height = 0, width = .5)+labs(title="Ambrosia")


#plotter elw istedenfor pnw. rplot09

ggplot(summarystats.am,aes(x=initiating_sex,y=elw,colour=sex, shape = mating_system)) +

  geom_jitter(height = 0, width = .5)+labs(title="Ambrosia beetles, elytra width", x="Initiating sex", y="Elytra width, µm", colour="Sex", shape="Mating system")+

  scale_x_discrete(labels=c("Female","Male"))+

  scale_colour_discrete(labels=c("Female", "Male"))+
```

```
    scale_shape_discrete(breaks=c("monogynous", "mild_polygynous", "polygynous"), labels=c("Monogynous", "Mild
polygynous", "Polygynous"))
```

#plotter for mating system istedet for init sex

```
ggplot(summarystats.am,aes(x=mating_system,y=elw,colour=sex, shape=initiating_sex))+

  geom_jitter(height=0,width=.5)+labs(title="Ambrosia", x="Mating system", y="Elytra width", colour="Sex", shape="Initiating
sex")+

  scale_x_discrete(breaks=c("monogynous","mild_polygynous", "polygynous"),

            labels=c("Monogynous", "Mild polygynous", "Polygynous"),

            limits=c("monogynous", "mild_polygynous", "polygynous"))+

  scale_colour_discrete(labels=c("Female", "Male"))+

  scale_shape_discrete(labels=c("Female", "Male"))
```

#ratios with errobars. how to add jitter? rplot06

```
ggplot(am.df,aes(x=species,y=rat,colour=sex, shape=initiating_sex))+

  stat_summary(fun.y=mean, geom="point")+

  stat_summary(fun.data=mean_cl_normal, geom="errorbar", na.rm=TRUE, width=0.3)+

  labs(title="Ambrosia beetles, length/width ratios", y="Elytra length/ Elytra width", x="Species", colour="Sex", shape="Initiating
sex")+

  scale_colour_discrete(labels=c("Female", "Male"))+

  scale_shape_discrete(labels=c("Female", "Male"))+

  theme(axis.text.x=element_text(angle = 90, hjust = 0))
```

#tester om forskjellige

```
t.test(elw~initiating_sex,summarystats.am)
```

#Lager sexual dimorphism index-verdiene. -(1:5) gjør at kolonne1-5fjernes

```
sdi.am <- ddply(summarystats.am, .(species,mating_system,initiating_sex,feeding_type),function(x){

  x[x$sex=="m",-(1:5)]/x[x$sex=="f",-(1:5)]

})
sdi.am
```

#plotter elw SDI. #rplot04

```
ggplot(sdi.am,aes(x=initiating_sex,y=elw, shape = mating_system))+

  geom_point()+
```

labs(title="Ambrosia beetles, elytra ratios", y="Mean female elw/mean male elw", x="Initiating sex", shape="Mating system")+

scale_shape_discrete(breaks=c("monogynous", "mild_polygynous", "polygynous"), labels=c("Monogynous", "Mild polygynous", "Polygynous"))+

scale_x_discrete(labels=c("Female", "Male"))

#samme som over, bare for elw-mating system

ggplot(sdi.am,aes(x=mating_system,y=elw, shape = initiating_sex))+

geom_point()+

labs(title="Ambrosia sex-ratios", y="Mean female elw/mean male elw", x="Initiating sex", shape="Initiating sex")+

scale_x_discrete(limits=c("monogynous", "mild_polygynous", "polygynous"),

       labels=c("Monogynous", "Mild polygynous", "Polygynous"))+

scale_shape_discrete(labels=c("Female", "Male"))

#tester om forskjellig

t.test(elw~initiating_sex,sdi.am)

#Plotter for BARKBILLER, simpelt boxplot

boxplot(bark.df$pnw~bark.df$sex, main="Bark beetle boxplot", xlab="Sex", ylab="Pronotum width")

#plotter bedre boxplot,

plot2 <- ggplot(bark.df, aes(x=sex,y=pnw)) +geom_boxplot()+facet_wrap(~species)+labs(title="Bark beetles")

plot2

#plotter enda litt finere. this is perf now

ggplot(bark.df, aes(x=pnl,y=pnw, colour = sex))+

geom_point()+facet_wrap(~species) +

labs(x="Pronotum length, µm",y="Pronotum width, µm", colour="Sex",title="Bark beetles")+

scale_colour_discrete(labels=c("Female", "Male"))

#Calculating means dataframe-dataframe plyfunction. colMeans tar gjennomsnitt av de gitte kolonnene

summarystats.bb <- ddply(bark.df, .(species,sex,mating_system,initiating_sex,feeding_type),function(x){

xb <- x[, c("ell","elw","pnl","pnw", "rat")]

cmb <- colMeans(xb, na.rm = TRUE)

```r
  sdsb <- colwise(sd)(xb, na.rm = TRUE)

  cvb <- sdsb / cmb

  data.frame(as.list(c(cmb, cvb)))

})


cvtestb <- ddply(summarystats.bb, .(species,mating_system,initiating_sex,feeding_type),function(x){

  x[x$sex=="m",-(1:5)]/x[x$sex=="f",-(1:5)]

})

cvtestb


cvtesta <- ddply(summarystats.am, .(species,mating_system,initiating_sex,feeding_type),function(x){

  x[x$sex=="m",-(1:5)]/x[x$sex=="f",-(1:5)]

})

cvtesta


summarystats.main <- ddply(data.df, .(species,sex,mating_system,initiating_sex,feeding_type),function(x){

  xm <- x[, c("ell","elw","pnl","pnw", "rat")]

  cmm <- colMeans(xm, na.rm = TRUE)

  sdsm <- colwise(sd)(xm, na.rm = TRUE)

  cvm <- sdsm/cmm

  data.frame(as.list(c(cmm, cvm)))

  })


cvtestmain <- ddply(summarystats.main, .(species,mating_system,initiating_sex,feeding_type),function(x){

  x[x$sex=="m",-(1:5)]/x[x$sex=="f",-(1:5)]

})


#testing if CV female/male of elw is different between mating systems

maintest.lm <- lm(elw.1~mating_system,cvtestmain)

anova(maintest.lm)

summary(maintest.lm)


t.test(cvtestb$elw.1,cvtesta$elw.1)

#CV difference between sexes in ambrosia beetles is not significantly different from bark beetles, elw
```

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```
#t test

t.test(summarystats.bb$elw.1,summarystats.am$elw.1)

t.test(summarystats.bb$elw.1,summarystats.am$ell.1)

t.test(summarystats.bb$elw.1,summarystats.am$pnw.1)

t.test(summarystats.bb$elw.1,summarystats.am$pnl.1)


#Plotter, jitter gjør at punktene flytter seg litt fra der de er

ggplot(summarystats.bb,aes(x=initiating_sex,y=pnw,colour=sex, shape = mating_system)) + geom_jitter(height = 0, width =
.5)+labs(title="Bark beetles")


#plotter elw istedenfor pnw. THIS IS PERF NOW except for order of legends, fix in paint. rplot03

ggplot(summarystats.bb,aes(x=initiating_sex,y=elw, shape = mating_system,colour=sex)) +

  labs(colour="Sex", shape="Mating system")+

  geom_jitter(height = 0, width = .5)+labs(title="Bark beetles, elytra width", x="Initiating sex", y="Elytra width, µm")+

  scale_shape_discrete(breaks=c("monogynous", "mild_polygynous","polygynous"),

              labels=c("Monogynous", "Mild Polygynous", "Polygynous"))+

  scale_colour_discrete(labels=c("Female","Male"))+

  scale_x_discrete(labels=c("Female", "Male"))


#plotter for mating system istedenfor init sex THIS IS PERF NOW

ggplot(summarystats.bb,aes(x=mating_system,y=elw, shape = initiating_sex,colour=sex)) +

  geom_jitter(height=0,width=.3)+

  labs(title="Bark beetles", x="Mating system", y="Elytra width, µm", colour="Sex", shape="Initiating sex")+

    scale_x_discrete(breaks=c("monogynous","mild_polygynous", "polygynous"),

              labels=c("Monogynous","Mild polygynous", "Polygynous"),

              limits=c("monogynous", "mild_polygynous", "polygynous"))+

              scale_shape_discrete(labels=c("Female", "Male"))+

              scale_colour_discrete(labels=c("Female", "Male"))

elbb.lm <- aov(elw~mating_system,summarystats.bb)


#tester om forskjellen er signifikant

summary(elbb.lm)

tuk2 <- TukeyHSD(elbb.lm)

tuk2
```

```
#plotter for pnw

ggplot(summarystats.bb,aes(x=mating_system,y=pnw,colour=sex,
shape=initiating_sex))+geom_jitter(height=0,width=.5)+labs(title="Bark beetles")


#tester om størrelsesforskjell mellom f init og m init er signifikant

t.test(elw~initiating_sex,summarystats.bb)


#plotter for ratios

ggplot(summarystats.bb,aes(x=species,y=rat,colour=sex, shape=initiating_sex))+geom_point()+labs(title="Bark-ratios")


#PRØVER MEG MED ERROR-BARS. fixer denne kjempefin. #rplot01

ggplot(bark.df,aes(x=species,y=rat,colour=sex, shape=initiating_sex))+stat_summary(fun.y=mean, geom="point")+

stat_summary(fun.data=mean_cl_normal, geom="errorbar", na.rm=TRUE, width=.3)+

labs(title="Bark beetles, length/width ratios", x="Species", y="Elytra length/elytra width", colour="Sex", shape="Initiating sex")+

scale_colour_discrete(labels=c("Female", "Male"))+

  scale_shape_discrete(labels=c("Female","Male"))+

  theme(axis.text.x=element_text(angle = 90, hjust = 0))


#Lager sexual dimorphism index-verdiene. -(1:5) gjør at kolonne1-5fjernes. males delt på females, >1, males størst

sdi.bb <- ddply(summarystats.bb, .(species,mating_system,initiating_sex,feeding_type),function(x){

  x[x$sex=="m",-(1:5)]/x[x$sex=="f",-(1:5)]

})

sdi.bb


#Plotter SDI for BB. rplot02

ggplot(sdi.bb,aes(x=mating_system,y=elw, shape=initiating_sex))+

  geom_jitter(height=0, width=.3)+

  labs(title="Bark beetles, elytra ratios", y="Female/male elytra width", x="Mating system", shape="Initiating sex")+

  scale_x_discrete(breaks=c("monogynous","mild_polygynous", "polygynous"),

          labels=c("Monogynous","Mild polygynous", "Polygynous"),

          limits=c("monogynous", "mild_polygynous", "polygynous"))+

  scale_shape_discrete(labels=c("Female", "Male"))


bbsr.lm <- aov(elw~mating_system,sdi.bb)
```

```
summary(bbsr.lm)

tuk1 <- TukeyHSD(bbsr.lm)

tuk1


####Plots

#1Bark beetles, elytra width

ggplot(summarystats.bb,aes(x=initiating_sex,y=elw, shape = mating_system,colour=sex)) +

  labs(colour="Sex", shape="Mating system")+

  geom_jitter(height = 0, width = .5)+labs(x="Initiating sex", y="Elytra width, µm")+

  scale_shape_discrete(breaks=c("monogynous", "mild_polygynous","polygynous"),

                  labels=c("Monogynous", "Mild Polygynous", "Polygynous"))+

  scale_colour_discrete(labels=c("Female","Male"))+

  scale_x_discrete(labels=c("Female", "Male"))


#1Ambrosia elytra width

ggplot(summarystats.am,aes(x=initiating_sex,y=elw,colour=sex, shape = mating_system)) +

  geom_jitter(height = 0, width = .5)+labs(x="Initiating sex", y="Elytra width, µm", colour="Sex", shape="Mating system")+

  scale_x_discrete(labels=c("Female","Male"))+

  scale_colour_discrete(labels=c("Female", "Male"))+

  scale_shape_discrete(breaks=c("monogynous", "mild_polygynous", "polygynous"), labels=c("Monogynous", "Mild
polygynous", "Polygynous"))


#2Bark beetles, elytra ratios

ggplot(sdi.bb,aes(x=mating_system,y=elw, shape=initiating_sex))+

  geom_jitter(height=0, width=.3)+

  labs(y="Mean male/female elytra width", x="Mating system", shape="Initiating sex")+

  scale_x_discrete(breaks=c("monogynous","mild_polygynous", "polygynous"),

          labels=c("Monogynous","Mild polygynous", "Polygynous"),

          limits=c("monogynous", "mild_polygynous", "polygynous"))+

  scale_shape_discrete(labels=c("Female", "Male"))


#2Ambrosia, elytra

ggplot(sdi.am,aes(x=mating_system,y=elw, shape = initiating_sex))+

  geom_point()+
```

```
labs(y="Mean male/female elytra width", x="Mating system", shape="Initiating sex")+
scale_x_discrete(limits=c("monogynous", "mild_polygynous", "polygynous"),
        labels=c("Monogynous", "Mild polygynous", "Polygynous"))+
scale_shape_discrete(labels=c("Female", "Male"))
```

```
#3Bark beetles length/width ratios
ggplot(bark.df,aes(x=species,y=rat,colour=sex, shape=initiating_sex))+stat_summary(fun.y=mean, geom="point")+
 stat_summary(fun.data=mean_cl_normal, geom="errorbar", na.rm=TRUE, width=.3, position="dodge")+
 labs(x="Species", y="Elytra length/elytra width", colour="Sex", shape="Initiating sex")+
 scale_colour_discrete(labels=c("Female", "Male"))+
 scale_shape_discrete(labels=c("Female","Male"))+
 theme(axis.text.x=element_text(angle = 90, hjust = 0))
```

```
#3Ambrosia length/width ratios
ggplot(am.df,aes(x=species,y=rat,colour=sex, shape=initiating_sex))+
 stat_summary(fun.y=mean, geom="point")+
 stat_summary(fun.data=mean_cl_normal, geom="errorbar", na.rm=TRUE, width=0.3)+
 labs(y="Elytra length/elytra width", x="Species", colour="Sex", shape="Initiating sex")+
 scale_colour_discrete(labels=c("Female", "Male"))+
 scale_shape_discrete(labels=c("Female", "Male"))+
 theme(axis.text.x=element_text(angle = 90, hjust = 0))
```