

# Sex-specific inbreeding depression: A meta-analysis

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## Section I. Moderators included in the meta-analysis.

### 1a. Descriptions of continuous moderators for meta-regression models.

Continuous moderator	Description
Sexual size dimorphism	<p>Males are generally expected to be under stronger sexual selection due to sex-specific differences in gametic investment (i.e., anisogamy, Parker <i>et al.</i> 1972) and because males typically experience greater variance in reproductive success than females (Wade 1979; Janicke <i>et al.</i> 2016). Deleterious alleles exposed to inbreeding may make males more sensitive to inbreeding depression either through purging or directional dominance being stronger on males (Wolak &amp; Keller 2014; Grieshop <i>et al.</i> 2021).</p> <p>Body size is considered a sexually selected trait as it may confer an advantage during episodes of sexual selection (pre, postcopulatory) and can be used as a proxy for sexual selection (Janicke &amp; Fromonteil 2021).</p> <p>Sexual size dimorphism for the species included in the study was calculated following Janicke and Fromonteil (2021). To do so, body size (body length, body mass, thorax length, wing length, elytra length, pronotum length) was used to calculate sexual size dimorphism:</p> $SSD = \ln \left( \frac{\text{male size}}{\text{female size}} \right)$ <p>where positive or negative values indicate species with males or females being the larger sex, respectively.</p>
Inbreeding coefficient	<p>Coefficient of inbreeding (probability of two alleles at a random chosen locus being identical by descent). Comparison of outbred <math>F = 0</math> vs inbred individuals <math>F = 0.125 - 0.785</math>.</p> <p>The costs of inbreeding depression are predicted to be higher when the coefficients of inbreeding are highest (Charlesworth &amp; Willis 2009), and so individuals with a higher inbreeding coefficient were expected to show stronger inbreeding depression.</p>
Publication Year	Year of publication, as extracted from Web of Science or Scopus.

## Ib. Description of categorical moderators for meta-regression models.

Categorical moderator	Category	Description
Sex		Males and females can be differently affected by inbreeding depression. Different processes may lead to non-mutually exclusive outcomes (sexual selection, heterogamety, dominance, sexual conflict) as to which sex may be more sensitive to inbreeding depression.
	Male	Trait measured in male individuals.
	Female	Trait measured in female individuals.
Heterogamety		Sex chromosomes are heteromorphic in many species, leading to one sex carrying a heterogamous set of sex chromosomes (e.g. XY males in XY systems and ZW females in ZW systems) and the other a homozygous set (e.g. XX females in XY systems and ZZ males in ZW systems). Genes on the heterozygous sex chromosomes (e.g. XY males) cannot contribute to inbreeding depression, because deleterious recessive alleles on the sex chromosome cannot be masked by a second dominant allele and are thus expressed regardless of the degree of inbreeding (Agrawal 2011; Sultanova <i>et al.</i> 2018).
	Homogametic Heterogametic	Sex where sex chromosomes are the same (e.g. XX, ZZ). Sex where sex chromosomes are not the same (e.g. XY, ZW).
Stress		Inbreeding depression is expected to be exacerbated under stressful conditions (Armbruster & Reed 2005; Fox & Reed 2011). Stronger sexual selection on males is often associated with density dependence, which reflects more intense intraspecific competition (i.e., a stressful environment, Yun & Agrawal 2014). Yet, selection in males and females can align under stressful conditions (Martinossi-Allibert <i>et al.</i> 2017).
		Note that stressful conditions were determined as stressful based the description provided by the authors of the papers included in our data, and in most cases, there was a comparison between outbred and inbred individuals that were in stressful vs non stressful environments.
	No Yes	Traits were measured under non-stressful environments Traits were measured under stressful environments (temperature stress, chemical stress, competition, food stress, environmental complexity).
Traits		The effects of inbreeding depression on different types of traits will differ due to the genetic architecture of the traits (Bolund <i>et al.</i> 2010). For instance, life history traits and sexually selected traits are expected to suffer higher levels of inbreeding depression than morphological traits (Crnokrak & Roff 1999; Cotton <i>et al.</i> 2004). The interplay between directional selection and sex-specific inbreeding depression is not known, and therefore fitness related traits were examined.
	Body size	Effect size measured in body size or body weight.
	Mating	Effect size measured in number of copulations, mating duration, mating latency.
	Reproduction	Effect size measured in number of offspring, paternity success, fecundity, egg viability.
	Survival	Effect size measured in lifespan or longevity.

<p>Class</p> <p>Actinopterygii Arachnida Aves Gastropoda Insecta Mammalia Secernentea Teleostei</p>	<p>Taxonomic class species belong to. Much information on inbreeding depression come from model species, and is essential to know how general are patterns across taxonomic groups.</p>
<p>Fertilisation mode</p> <p>Internal External</p>	<p>Differences in the site of fertilisation may predict the extent of inbreeding depression and in turn affect the evolution of mating systems (Cohen 1996). External fertilisers share key life history traits with seed plants (low mobility, release of gametes into the environment) (Olsen <i>et al.</i> 2020), which may lead to external fertilisers being more sensitive to inbreeding depression.</p> <p>Trait measured in species with internal fertilisation.</p> <p>Trait measured in species with external fertilisation.</p>
<p>Reproductive mode</p> <p>Egg-laying Live-bearing</p>	<p>The mode of reproduction can affect how sensitive species are to inbreeding depression as allocation and investment of resources may differ. Whether males or females could be differentially affected by this inherent biological difference has not been addressed.</p> <p>Trait measured in species that lay eggs.</p> <p>Trait measured in species that give birth to live young.</p>

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## Section II. List of species included in the meta-analysis with their corresponding heterogamy.

Species	Female	Male	Family	Order	Class	Heterogametic system	Source
<i>Drosophila serrata</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila bunnanda</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila birchii</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila simulans</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila melanogaster</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila bipectinata</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila pseudoananassae</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila repleta</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Drosophila sulfurigaster</i>	homogametic	heterogametic	Drosophilidae	Diptera	Insecta	XX, XY	(Navara 2018)
<i>Teleopsis dalmanni</i>	homogametic	heterogametic	Diopsidae	Diptera	Insecta	XX, XY	(Warren <i>et al.</i> 2010)
<i>Aedes geniculatus</i>	homogametic	heterogametic	Culicidae	Diptera	Insecta	mm, Mm	(Koskinioti <i>et al.</i> 2021)
<i>Aedes albopictus</i>	homogametic	heterogametic	Culicidae	Diptera	Insecta	mm, Mm	(Craig & Hickey 1967)
<i>Heliconius erato</i>	heterogametic	homogametic	Nymphalidae	Lepidoptera	Insecta	ZW, ZZ	(Van Belleghem <i>et al.</i> 2018)
<i>Bicyclus anynana</i>	heterogametic	homogametic	Nymphalidae	Lepidoptera	Insecta	WZ, ZZ	(Van't Hof <i>et al.</i> 2008)
<i>Pieris napi</i>	heterogametic	homogametic	Pieridae	Lepidoptera	Insecta	ZW, ZZ	(Keehnen <i>et al.</i> 2018)
<i>Stator limbatus</i>	homogametic	heterogametic	Chrysomelidae	Coleoptera	Insecta	XX, XO	(Arnqvist <i>et al.</i> 2015)
<i>Callosobruchus maculatus</i>	homogametic	heterogametic	Chrysomelidae	Coleoptera	Insecta	XX, XO	(Savalli & Fox 1998)
<i>Phaedon cochleariae</i>	homogametic	heterogametic	Chrysomelidae	Coleoptera	Insecta	XX, XO	(Arnqvist <i>et al.</i> 2015)
<i>Euscepes postfasciatus</i>	homogametic	heterogametic	Curculionidae	Coleoptera	Insecta	XX, XO	(Suomalainen 1940)
<i>Ips pini</i>	homogametic	heterogametic	Curculionidae	Coleoptera	Insecta	XX, XO	(Sargent & Reid, 1999)
<i>Tenebrio molitor</i>	homogametic	heterogametic	Tenebrionidae	Coleoptera	Insecta	XX, XO	(Arnqvist <i>et al.</i> 2015)
<i>Tribolium castaneum</i>	homogametic	heterogametic	Tenebrionidae	Coleoptera	Insecta	XX, XO	(Arnqvist <i>et al.</i> 2015)
<i>Nicrophorus vespilloides</i>	homogametic	heterogametic	Silphidae	Coleoptera	Insecta	XX, XO	(Angus & Diaz, 1991)
<i>Narnia femorata</i>	homogametic	heterogametic	Coreidae	Hemiptera	Insecta	XX, XO	(Dutt 1959)
<i>Teleogryllus oceanicus</i>	homogametic	heterogametic	Gryllidae	Orthoptera	Insecta	XX, XO	(Moran <i>et al.</i> 2018)
<i>Teleogryllus commodus</i>	homogametic	heterogametic	Gryllidae	Orthoptera	Insecta	XX, XO	(Moran <i>et al.</i> 2018)
<i>Gryllobes sigillatus</i>	homogametic	heterogametic	Gryllidae	Orthoptera	Insecta	XX, XY	(Rao & Arora 1979)
<i>Forficula auricularia</i>	homogametic	heterogametic	Forficulidae	Dermaptera	Insecta	XX, XY	(Rankin & Palmer 2009)
<i>Stegodyphus lineatus</i>	homogametic	heterogametic	Eresidae	Araneae	Arachnida	X <sub>1</sub> X <sub>1</sub> X <sub>2</sub> X <sub>2</sub> , X <sub>1</sub> X <sub>2</sub> 0	(Cordellier <i>et al.</i> 2020)

<i>Rhizoglyphus robini</i>	homogametic	heterogametic	Acaridae	Sarcoptiformes	Arachnida	XX, XO	(Radwan 1995)
<i>Caenorhabditis remanei</i>	homogametic	heterogametic	Rhabditidae	Rhabditida	Secernentea	XX, XO	(Baird & Seibert 2013)
<i>Physa acuta</i>	NA	NA	Physidae	Hygrophila	Gastropoda		
<i>Poeciliopsis occidentalis</i>	heterogametic	homogametic	Poeciliidae	Cyprinodontiformes	Actinopterygii	XY, XX	(Yamamoto & Kajishima 1968)
<i>Gambusia holbrooki</i>	homogametic	heterogametic	Poeciliidae	Cyprinodontiformes	Actinopterygii	XX, XY	(Senior <i>et al.</i> 2013)
<i>Heterandria formosa</i>	NA	NA	Poeciliidae	Cyprinodontiformes	Actinopterygii		
<i>Poecilia reticulata</i>	homogametic	heterogametic	Poeciliidae	Cyprinodontiformes	Actinopterygii	XX, XY	(Tomohisa <i>et al.</i> 2005)
<i>Pelvicachromis taeniatus</i>	homogametic	heterogametic	Cichlidae	Cichliformes	Actinopterygii	XX, XY	(Pandian 2011)
<i>Oreochromis niloticus</i>	homogametic	heterogametic	Cichlidae	Cichliformes	Actinopterygii	XX, XY	(Lee <i>et al.</i> 2003)
<i>Danio rerio</i>	NA	NA	Cyprinidae	Cypriniformes	Teleostei		
<i>Microtus oeconomus</i>	homogametic	heterogametic	Cricetidae	Rodentia	Mammalia	XX, XY	(Raman & Das 1991)
<i>Microtus ochrogaster</i>	homogametic	heterogametic	Cricetidae	Rodentia	Mammalia	XX, XY	(Borodin <i>et al.</i> 2012)
<i>Peromyscus leucopus</i>	homogametic	heterogametic	Cricetidae	Rodentia	Mammalia	XX, XY	(Waters <i>et al.</i> 2007)
<i>Peromyscus polionotus</i>	homogametic	heterogametic	Cricetidae	Rodentia	Mammalia	XX, XY	(Waters <i>et al.</i> 2007)
<i>Parotomys littledalei</i>	homogametic	heterogametic	Muridae	Rodentia	Mammalia	XX, XY	(Waters <i>et al.</i> 2007)
<i>Mus musculus domesticus</i>	homogametic	heterogametic	Muridae	Rodentia	Mammalia	XX, XY	(Raman & Das 1991)
<i>Serinus canaria</i>	heterogametic	homogametic	Fringillidae	Passeriformes	Aves	ZW, ZZ	(Doosti <i>et al.</i> 2009)

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### Section III. List of species included in the meta-analysis with their corresponding sexual size dimorphism.

Species	Family	Order	Class	Size Dimorphism	Trait measured	Source
<i>Drosophila serrata</i>	Drosophilidae	Diptera	Insecta	-0.0561	wing size	(Liefting <i>et al.</i> 2009)
<i>Drosophila bunnanda</i>	Drosophilidae	Diptera	Insecta			
<i>Drosophila birchii</i>	Drosophilidae	Diptera	Insecta	0.0654	wing size	(Kellermann <i>et al.</i> 2007)
<i>Drosophila simulans</i>	Drosophilidae	Diptera	Insecta	-0.1088	thorax length	(Pitnick <i>et al.</i> 1995)
<i>Drosophila melanogaster</i>	Drosophilidae	Diptera	Insecta	-0.1178	thorax length	(Pitnick <i>et al.</i> 1995)
<i>Drosophila bipectinata</i>	Drosophilidae	Diptera	Insecta	-0.2746	wing size	(Imasheva <i>et al.</i> 1999)
<i>Drosophila pseudoananassae</i>	Drosophilidae	Diptera	Insecta			
<i>Drosophila repleta</i>	Drosophilidae	Diptera	Insecta			
<i>Drosophila sulfurigaster</i>	Drosophilidae	Diptera	Insecta	-0.0135	wing length	(Neethu & Harini 2014)
<i>Teleopsis dalmanni</i>	Diopsidae	Diptera	Insecta	0.0342	thorax length	(Prokop <i>et al.</i> 2010)
<i>Aedes geniculatus</i>	Culicidae	Diptera	Insecta	-0.5251	body mass	(Bradshaw & Holzapfel 1992)
<i>Aedes albopictus</i>	Culicidae	Diptera	Insecta	-0.1867	wing size	(Sánchez <i>et al.</i> 2017)
<i>Heliconius erato</i>	Nymphalidae	Lepidoptera	Insecta	-0.0028	hind wing length	(Klein & de Araújo 2013)
<i>Bicyclus anynana</i>	Nymphalidae	Lepidoptera	Insecta	-0.2343	pupal mass	(Dierks <i>et al.</i> 2012)
<i>Pieris napi</i>	Pieridae	Lepidoptera	Insecta	0.0246		(Stjernholm & Karlsson 2000)
<i>Stator limbatus</i>	Chrysomelidae	Coleoptera	Insecta	0.0350	body mass	(Stillwell & Fox 2009)
<i>Callosobruchus maculatus</i>	Chrysomelidae	Coleoptera	Insecta	-0.0478	elytron length	(Colgoni & Vamosi 2006)
<i>Phaedon cochleariae</i>	Chrysomelidae	Coleoptera	Insecta	-0.4523	body mass	(Müller <i>et al.</i> 2016)
<i>Euscepes postfasciatus</i>	Curculionidae	Coleoptera	Insecta	-0.0175	elytra length	(Kumano <i>et al.</i> 2010)
<i>Ips pini</i>	Curculionidae	Coleoptera	Insecta	0.0118	body size	(Foelker & Hofstetter 2014)
<i>Tenebrio molitor</i>	Tenebrionidae	Coleoptera	Insecta	0.0268	body mass	(Rantala <i>et al.</i> 2011)
<i>Tribolium castaneum</i>	Tenebrionidae	Coleoptera	Insecta	-0.0196	protonum width	(Conner & Via 1992)
<i>Nicrophorus vespilloides</i>	Silphidae	Coleoptera	Insecta	-0.0253	elytra length	(Otronen 1988)
<i>Narnia femorata</i>	Coreidae	Hemiptera	Insecta	-0.0824	protonum width	(Allen & Miller 2017)
<i>Teleogryllus oceanicus</i>	Gryllidae	Orthoptera	Insecta	0.0507	protonum width	(Nystrand <i>et al.</i> 2011)
<i>Teleogryllus commodus</i>	Gryllidae	Orthoptera	Insecta	0.0697	body mass	(Drayton <i>et al.</i> 2011)
<i>Gryllobes sigillatus</i>	Gryllidae	Orthoptera	Insecta	-0.0673	femur length	(Galicia <i>et al.</i> 2014)
<i>Forficula auricularia</i>	Forficulidae	Dermaptera	Insecta	0.2136	elytra length	(Radesäter & Halldórsdóttir 1993)
<i>Stegodyphus lineatus</i>	Eresidae	Araneae	Arachnida	-0.0866	body size	(Schneider 1997)



<i>Rhizoglyphus robini</i>	Acaridae	Sarcoptiformes	Arachnida	-0.2016	body size	(Deere <i>et al.</i> 2015)
<i>Caenorhabditis remanei</i>	Rhabditidae	Rhabditida	Secernentea	NA		
<i>Physa acuta</i>	Physidae	Hygrophila	Gastropoda	NA		
<i>Poeciliopsis occidentalis</i>	Poeciliidae	Cyprinodontiformes	Actinopterygii	-0.3331	body size	(Constanz 1975)
<i>Gambusia holbrooki</i>	Poeciliidae	Cyprinodontiformes	Actinopterygii	-0.3506	body size	(Bisazza & Pilastro 1997)
<i>Heterandria formosa</i>	Poeciliidae	Cyprinodontiformes	Actinopterygii	-0.2345	body size	(Bisazza & Pilastro 1997)
<i>Poecilia reticulata</i>	Poeciliidae	Cyprinodontiformes	Actinopterygii	-0.3523	body size	(Bisazza & Pilastro 1997)
<i>Pelvicachromis taeniatus</i>	Cichlidae	Cichliformes	Actinopterygii	0.3538	body size	(Meuthen <i>et al.</i> 2018)
<i>Oreochromis niloticus</i>	Cichlidae	Cichliformes	Actinopterygii	0.0657	body size	(Nguyen <i>et al.</i> 2007)
<i>Danio rerio</i>	Cyprinidae	Cypriniformes	Teleostei	-0.0843	body size	(Uusi-Heikkilä <i>et al.</i> 2012)
<i>Microtus oeconomus</i>	Cricetidae	Rodentia	Mammalia	0.0180	body mass	(Tast 1972)
<i>Microtus ochrogaster</i>	Cricetidae	Rodentia	Mammalia	0.0732	body mass	(Dewsbury <i>et al.</i> 1980)
<i>Peromyscus leucopus</i>	Cricetidae	Rodentia	Mammalia	0.0723	body mass	(Dewsbury <i>et al.</i> 1980)
<i>Peromyscus polionotus</i>	Cricetidae	Rodentia	Mammalia	-0.0192	body mass	(Dewsbury <i>et al.</i> 1980)
<i>Parotomys littledalei</i>	Muridae	Rodentia	Mammalia	0.1955	body mass	(Pillay 2002)
<i>Mus musculus domesticus</i>	Muridae	Rodentia	Mammalia	0.1405	body mass	(Dewsbury <i>et al.</i> 1980)
<i>Serinus canaria</i>	Fringillidae	Passeriformes	Aves	0.0223	tarsus length	(de Boer <i>et al.</i> 2016)

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