

# Fisher & Salguero-Gomez reproductive death final with tables

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**Reproductive death: pathways to obligate semelparity in female and male animals and plants**

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Key words/phrases

Iteroparity, life history, reproductive death, semelparous, terminal investment, matrophagy

## 18 **Abstract**

19

20 Organisms that breed only once are semelparous. Theoretical frameworks to explain the  
21 evolution of semelparity are based on the premise of reproductive costs to future survival,  
22 and emphasize either a high risk of death after breeding for environmental reasons (the  
23 demographic model) or disproportionate fitness benefits at higher reproductive effort (the  
24 reproductive effort model). Here, we review environmental drivers that increase risk of post-  
25 reproductive death, conditions in which lethal reproductive efforts are beneficial, biological  
26 mechanisms of death in semelparous organisms, and of reproductive capacity loss in obligate  
27 semelparous females and males. We find that age-specific mortality risk is overwhelmingly  
28 the dominant driver of facultative and obligate semelparity in animals and plants: most  
29 species follow predictions of the demographic model. We find that female semelparous  
30 organisms die from diverse mechanisms that cause somatic damage as they increase  
31 reproductive output. Semelparous female animals are nearly all predators, suggesting a  
32 nutritional constraint on fecundity associated with the viability of the semelparous life history  
33 strategy. We propose that in species in which only males are semelparous, the driver is  
34 always post-mating male sexual competition. Sexual conflict occurs because females escalate  
35 sperm competition to gain fitness benefits, and males can increase reproductive success  
36 through a mechanism of competition that causes lethal somatic damage, typically involving  
37 extreme investment in mate-guarding. In organisms with obligate male-only semelparity the  
38 mechanism of death is often decoupled from the mechanism of reproductive capacity loss,  
39 which typically occurs at sexual maturity. We propose that this pre-breeding loss of future  
40 reproductive capacity is associated with a post-mating sexual competition strategy analogous  
41 to 'capital breeding', in which males keep a lifetime store of gametes near the outside of the  
42 body to transfer quickly in a single mating period. We suggest that male-only semelparity is

43 consistent with the reproductive effort model. We find no examples of semelparity in plants  
44 associated with pollination costs. We suggest that the absence of a potential mechanism of  
45 sexual selection that damages somatic tissue to the advantage of male fitness in plants  
46 precludes the evolution of semelparity only in the male function.

47 Semelparity is defined as the life history strategy in which an organism breeds only once.  
48 This general term does not tell us whether the organism *can* breed more than once, only that  
49 it does not. Some taxa have evolved mechanisms that prevent further reproduction after their  
50 first reproductive bout (obligate semelparity). Others typically reproduce once, but could  
51 reproduce repeatedly (facultative semelparity). Parity (Lt. *parus* = birth) describes the  
52 number of reproductive events between an organisms' age at maturity and its death, and is a  
53 measure of how dispersed reproductive events are across lifespan (Hughes 2017).  
54 Semelparity is one extreme of this continuum, while iteroparity describes all other strategies  
55 of more dispersed temporal breeding throughout life (Tuljapurkar et al. 2009). In most  
56 typically semelparous organisms, semelparity is facultative and individuals can distribute  
57 reproduction across more episodes when conditions favour iteroparity. Iteroparity is thought  
58 to be the ancestral state in most animal and plant Orders and Families (Friedman 2020), and  
59 semelparity is widespread but uncommon across the tree of life at the genus and species level  
60 (Roff 1992).  
61 Although the definition of semelparity says nothing about why an organism may breed only  
62 once, the adaptive life history strategy of semelparity is always entangled in an organisms's  
63 investment in reproduction (Charnov and Schaffer, 1973). Semelparity can be viewed as a  
64 special case of terminal investment, which occurs when an individual perceives  
65 environmental cues suggesting a low probability of future breeding. When residual  
66 reproductive value (the remaining reproduction expected in an organism's life) is low,  
67 unrestrained reproductive effort can maximise fitness. Indeed, terminal investment increases  
68 fitness if there is a survival cost of reproduction, and when concentrated investment in  
69 breeding kills the parent this is 'reproductive death' (Kern and Gems 2022). Semelparity  
70 resulting from reproductive death is thus terminal investment in the first reproductive event.

71

72 The goal of this review is to integrate research findings on the drivers and associated  
73 mechanisms of semelparity in animals and plants, to establish if and why males and females  
74 have distinct evolutionary pathways to obligate semelparity.

75

76 The framework of drivers of fitness benefits, mechanisms of death, and mechanisms of  
77 reproductive capacity loss

78

79 We consider three levels of explanation for reproductive death as an evolved strategy in  
80 males and females: 1) The ultimate driver. What environmental or biological cause results in  
81 a greater fitness benefit of temporally unrestrained reproductive effort than of restrained  
82 effort partitioned into several reproductive events? 2) The proximate cause of death. What  
83 environmental or biological mechanism kills the semelparous organism? 3) The mechanism  
84 of reproductive capacity loss. What biological mechanism sterilises an organism in the final  
85 step to obligate semelparity?

86

87 We collate studies that investigate the drivers and mechanisms of semelparity in animals and  
88 plants that show evidence of either facultative or obligate semelparity (Appendix 1: Tables  
89 S1-10). Most field and captive studies are at the taxonomic level of species, and we report  
90 tests of predictions in individual species when available. Some cases in our tables focus on  
91 one member of a speciose semelparous clade and infer a more general pattern (*e.g.*, bamboo  
92 or coleoid cephalopods) or interpret patterns in a clade in which some species show obligate  
93 semelparity in one or both sexes (such as the Dermapteran insect family Forficulidae).

94

95 Trade-offs between reproduction and survival reflect a continuous axis of parity, along which  
96 organisms disperse or concentrate reproductive effort throughout their lives (Hughes 2017).

97 In their investigation of drivers, the authors of models to investigate the fitness benefits of  
98 semelparity (Charnov and Schaffer 1973, Young and Augspurger 1991, Charlesworth 1994,  
99 Tuljapurkar et al. 2009) have not generally considered how different sexes invest differently  
100 in reproduction, or distinguished between facultative and obligate semelparity. We therefore  
101 lack a general mechanistic understanding of how obligate semelparity and sex differentiation  
102 in semelparity evolves. Understanding sex-specific pathways to obligate semelparity is  
103 important because sex-biased semelparity can lead to sex-ratio differences and large  
104 fluctuations in population size and structure, with important consequences for the ecology,  
105 evolution, and conservation of species (Keeley and Bond 1999, Fisher et al. 2013, Salguero-  
106 Gomez 2017, Fisher et al. 2018, Cunningham et al. 2021), and for understanding limitations  
107 of selection in commercially important semelparous fisheries, and domestic species (Baer  
108 2005, Campton 2005, Deiner et al. 2007).

109

#### 110 The two main classes of driver models

111

112 Two dominant models that emphasize different drivers of semelparity are the **demographic**  
113 **model** and the **reproductive effort model**. The demographic model predicts that semelparity  
114 will be favoured when adult post-breeding mortality risk is high relative to juvenile mortality  
115 risk (Fig. 1), including when juvenile mortality risk or reproduction are density-dependent  
116 (Charnov and Schaffer 1973, Charlesworth 1994), provided that post-breeding mortality risk  
117 increases with increasing reproductive effort (Schaffer 1974, Takada 1995). In other words,  
118 when the chance of future reproduction is low enough, natural selection will favour strategies  
119 where an organism stops withholding resources for future reproduction and instead uses all of  
120 its available resources in a single reproductive event at the expense of its own future survival  
121 (Young and Augspurger 1991).

122

123 Quantitative models show that escalating (non-linear) fitness benefits of intense reproduction  
124 alone can also favour the evolution of semelparity (Bell 1980, Takada 1995). The  
125 reproductive effort model predicts that semelparity is adaptive when fitness benefits of  
126 reproduction increase disproportionately at high levels of reproductive effort, or if a survival  
127 cost of reproduction has most effect at low reproductive effort (Schaffer and Gadgil 1975). A  
128 game theory assessment by Takada (1995) suggested that the reproductive effort model  
129 applies under conditions of density dependence.

130

### 131 Drivers of semelparity

132

133 We find that, in 91 published studies that tested predictions of a driver with a plausible basis  
134 in natural selection on individuals of >60 species (Appendix 1: Tables S1-10), researchers  
135 suggested four ultimate reasons why semelparity confers greater fitness than a strategy of  
136 restrained, temporally distributed investment in reproduction. We summarise these overall  
137 drivers here, and discuss species examples in the sections that follow:

138 1) A higher adult than juvenile mortality risk, caused by a compulsory risky and strenuous  
139 breeding migration at maturity against the prevailing current, high risk of predation or  
140 parasitism from an efficient natural enemy that targets adults, or a hot and dry or fire-prone  
141 environment that poses an exceptionally high risk to large and mature individuals with  
142 indeterminate growth.

143 2) The constraint of food or pollinators needed for successful reproduction only being  
144 available in a short breeding season, when adults are unlikely to survive the interval to the  
145 distant next possible reproductive season due to climatic conditions or natural enemies as  
146 above.

147 3) Intense sexual competition between males in the form of post-copulatory competition  
148 driven by sexual conflict, in which skewed fitness benefits increase disproportionately at high  
149 reproductive investment by males.

150 4) Intense intraspecific exploitation competition between clonal individuals in plants, in  
151 which fitness benefits increase disproportionately at high reproductive investment in  
152 propagules.

153

#### 154 Mechanisms of death in semelparous organisms

155

156 With the exception of a single published case, in which overheating was the mechanism of  
157 death in a facultatively semelparous mammal (Desert woodrat *Neotoma lepida*, Appendix 1:  
158 Table S3, (Smith and Charnov 2001)), death in semelparous organisms results from tissue  
159 loss: individual semelparous animals and plants die from mechanisms of somatic damage  
160 (that destroy their body tissue) gradually or suddenly through: starvation (e.g. Goldenrod crab  
161 spider *Misumena vatia*, Appendix 1: Table S1), autophagy (e.g. wild beet *Beta patula*,  
162 Appendix 1: Table S5), transfer of crucial tissue to reproductive parts or young (e.g. capelin  
163 *Mallotus villosus*, Appendix 1: Table S3), matrophagy- young eating their mothers (e.g.  
164 savanna Pseudoscorpion *Paratemnoides nidificator*, Appendix 1: Table S1), tissue  
165 investment in mate-guarding through sexual organs or body sections being removed to form  
166 mating plugs (e.g. St Andrew's cross spider *Argiope aemula*, Appendix 1: Table S8) or to  
167 facilitate male post-mating guarding (e.g. hermit spider *Nephilengys borbonica*, Appendix 1:  
168 Table S8), sexual cannibalism- females eating their mates (e.g. Chinese mantid *Tenodera*  
169 *sinensis*, Appendix 1: Table S7), energy investment in fighting and loss to injuries (e.g.  
170 Labord's dwarf chameleon *Furcifer labordi*, Appendix 1: Table S9), or loss to parasitoids as  
171 a result of maternal care behaviour (e.g. wolf spider *Geolycosa domifex*, Appendix 1: Table

172 S1). In obligate semelparous organisms, the manner of somatic damage is directly related to  
173 allocation to gestation and birth, flowering and seed production, or maternal care in females  
174 and tissue allocation to sperm transfer in males (Appendix 1: Tables S2, 4, 6, 8, and 10).

175

#### 176 Mechanisms of sterility in obligate semelparous organisms

177

178 Obligate semelparous organisms have idiosyncratic physiological processes and/or behaviour  
179 to prevent future reproduction. In dioecious species, the mechanism of loss of future  
180 reproductive capacity before death often occurs in an immature part of the life cycle long  
181 before the proximate mechanism of death, and operates at maturity, or at mating. In females,  
182 the mechanism of sterility occurs typically at the gamete investment stage and sometimes at  
183 the offspring investment stage of the life cycle (Appendix 1: Tables S2 and 4), and in males  
184 typically at the mating stage and often at the gamete investment stage (Appendix 1: Tables S8  
185 and 10). Future sterility in obligate semelparous animals results from: ovaries degrading  
186 irreversibly after production of two clutches in species that have capacity to only raise one  
187 clutch to independence (e.g. the Japanese crab spider, *Lysiteles coronatus*; Appendix 1: Table  
188 S2), ovaries degrading irreversibly after females produce one clutch (e.g. the Australian crab  
189 spider, *Australomisidia ergandros*; Japanese hump earwig, *Anechura harmandi*; octopodid  
190 mollusc species; Appendix 1: Table S2), the gut and organs dissolving irreversibly into fluid  
191 that is regurgitated or ejected to feed young that depend on this source of nutrition (e.g. the  
192 eresid spider, *Stegodyphus sarasinorus*; the nematode *Caenorhabditis elegans*; Appendix 1:  
193 Table S2), the gut and organs dissolving irreversibly through transfer of fat and protein from  
194 them to enable gamete development (e.g., European conger, eel *Conger conger*; river  
195 lamprey, *Lampetra fluviatilis*; Appendix 1: Table S4), gut, bones, and teeth dissolving  
196 irreversibly through transfer of fat, protein, and calcium from them to enable gamete

197 development (e.g., Japanese eel, *Anguilla japonica*; Appendix 1: Table S4), reproductive  
198 organs breaking or tearing off, being amputated or altered (inflated, distorted, *etc.*) either by  
199 the male or the female so they become unusable a second time (e.g., dark fishing spider,  
200 *Dolomedes tenebrosus*; European honey bee, *Apis mellifera*; Appendix 1: Table S8), testes  
201 degrading or ceasing spermatogenesis irreversibly before or at maturity so that all sperm are  
202 transferred to a storage location in or on the body before any mating opportunities (e.g.,  
203 North African comb-footed spider, *Tidarren argo*, Appendix 1: Table S8; brown antechinus,  
204 *Antechinus stuartii*, Appendix 1: Table S10). Sterility in obligate semelparous plants results  
205 from autophagy, such that critical tissue is irreversibly transferred to single-use reproductive  
206 structures (e.g., Desert agave, *Agave deserti*, Appendix 1: Table S6).

207

### 208 **Pathways to semelparity**

209

210 We find that the demographic model has wide support in animals and plants: age-specific  
211 mortality risk is the major driver of semelparity (Appendix 1: Tables S1-6). In contrast, the  
212 reproductive effort model has compelling support primarily in taxa with male semelparity  
213 and a mechanism of post-copulatory sexual selection. In these taxa, there is a non-linear  
214 association between fitness benefits and the expenditure required for high reproductive  
215 success (Appendix 1: Tables S7-10).

216

217 Loss of reproductive capacity before the breeding stage in obligate semelparous organisms  
218 has diverse energy-saving advantages that allow the organism to increase expenditure on  
219 reproduction. In males, the mechanism of obligate semelparity typically occurs during  
220 mating, and it sometimes includes both energy savings and non-energetic advantages in  
221 reproductive competition, such as manipulation of female behaviour, or compliance with

222 female manipulation of male behaviour (Andrade 1996, Fisher et al. 2006). Ways that loss of  
223 future reproductive capacity can benefit current reproductive effort in animals and plants  
224 include: feeding the reserve second clutch or trophic eggs to the current brood (e.g., the Black  
225 lace-weaver spider, *Amaurobius ferox*, Appendix 1: Table S2), feeding body tissue critical to  
226 future reproduction to the current brood (e.g., the isopod crustacean *Paracerceis sculpta*,  
227 Appendix 1: Table S2), mobilising body tissue critical to future reproduction for ovary,  
228 testes, or flower development or gamete and seed production (e.g., Pacific salmon,  
229 *Oncorhynchus* spp., Appendix 1: Table S3; evening primrose, *Oenothera* spp., Appendix 1:  
230 Table S5), limiting gamete production to a discrete time before the mating period so that  
231 more energy can be directed to sexual competition during the critical competitive window of  
232 the mating season (e.g., males of the dasyurid marsupial the red-tailed phascogale,  
233 *Phascogale calura*; males of the Anguillid fish the European eel *Anguilla anguilla*, Appendix  
234 Appendix 1: Table S10), partly amputating genitals to increase agility during sexual  
235 competition (e.g., North American comb-footed spider, *Tidarren sisypoides*, Appendix 1:  
236 Table S8), or amputating or mutilating genitals for redeployment as single-use mating plugs  
237 to potentially reduce competitor fertilizations and enhance their own paternity success (e.g.  
238 males of the yellow garden spider, *Argiope aurantia*; males of the Brazilian queenless  
239 ponerine ant, *Dinoponera quadriceps*, Appendix 1: Table S8).

240

#### 241 **Pathways to obligate semelparity in females**

242

243 The pathway to obligate semelparity in females can include diverse causes of adult-biased  
244 mortality as a driver, combined with a mechanism of investing body reserves in offspring  
245 fitness (Appendix 1: Tables S2 and 4). Female animals and monoecious plants transfer  
246 critical components of their body tissue to their young or flowers and seeds. Mother animals

247 starve or deplete their own stores of energy while guarding young to increase offspring  
248 survival by preventing predation, starvation, or infection (e.g. Mediterranean eresid spider,  
249 *Stegodyphus lineatus*; pentastomid insect, *Parastrachia japonensis*; pseudoscorpion,  
250 *Paratemnoides nidificator*, Appendix 1: Table S1; deep-sea megaleledonid octopus,  
251 *Graneledone boreopacifica*, Appendix 1: Table S2). Future sterility in obligate semelparous  
252 females results from ovaries degrading irreversibly after ovulation, or from the transfer of a  
253 finite component of their body tissue to one bout of flowering or gamete development (e.g.  
254 ovary development uses protein from muscles, connective tissue, the gut and the body wall in  
255 lampreys, Appendix 1: Table S4 (Larsen and Dufour 1993)). Consistent with maternal  
256 investment, the mechanism of future sterility operates either during gamete production or  
257 during maternal care in females, not during mating. Published studies of obligate semelparity  
258 in female animals did not always test or suggest a driver; however all tests that did suggest  
259 one favoured the explanation of adult-biased mortality (Appendix 1: Tables S2 and 4). For  
260 example, (Shuster 1991) proposed that the driver in the small marine isopod crustacean  
261 *Paracerceis sculpta* is a high mortality risk in adults while migrating between feeding  
262 (offshore algal beds) and breeding habitat (inside intertidal sponges)- adults are unlikely to  
263 survive multiple breeding migrations. Mature females cannot eat, and the maternal  
264 investment mechanism that kills the brooding mother is transfer of her lipid stores, organs,  
265 and muscle tissue to her first clutch of developing young as she broods them inside her body  
266 cavity.

267

268 Some authors suggest that extreme maternal care, such as matrophagy and starvation while  
269 brooding evolved because high maternal investment is necessary for offspring survival (e.g.  
270 in the Japanese sac spider, *Chiracanthium japonicum*, Appendix 1: Table S1). However, this  
271 explanation focuses on the phenomenon of reproductive death without addressing the

272 underlying mechanism. Indeed, extreme maternal care is not necessarily associated with  
273 semelparity, even if offspring cannot survive without such care. For example, no  
274 echinoderms are known to be semelparous (Pandian 2018), although some species brood  
275 young in their mouths and do not eat for up to nine months. The Antarctic sea star  
276 *Neosmilaster georgianus* depletes its energy stores during months of brooding and takes two  
277 years to accumulate enough body reserves to breed again (Bosch and Slattery 1999). Low  
278 post-brooding mortality risk must make this strategy viable. Similarly, masting in some  
279 iteroparous trees with high adult survivorship such as oaks involves forgoing successive  
280 reproductive windows to set seed intensively and synchronously every 4-7 years. The crucial  
281 question regarding reproductive death is not whether maternal investment through lethal  
282 somatic damage decreases offspring mortality risk. In terms of adaptive explanation, the issue  
283 is why females in obligate semelparous species would not obtain a greater fitness return from  
284 high but survivable investment, followed by a long interval between births.

285

286 The fact that the diverse environmental causes of adult-biased mortality are typically shared  
287 in males and females of the same species suggests that males of species that show female  
288 semelparity are also expected to be semelparous, or to have high adult mortality. Examples of  
289 shared environments that would have high mortality risk in post-reproductive adults  
290 attempting to breed a second time include arduous breeding migration routes (in eels,  
291 lampreys, Pacific salmon, and a marine isopod, Appendix 1: Tables S2 and 4), predation or  
292 parasitism from a natural enemy that targets adults of both sexes (in some spiders and the  
293 plant Houndstongue *Cynoglossum officinale*, Appendix 1: Tables S1 and 5), or a hot and dry  
294 or fire-prone environment that poses high risk to all large and mature individuals (the desert  
295 woodrat *Neotoma lepida*, Appendix 1: Table S3, and some plants including evening  
296 primroses *Oenothera*, Mount Kenya rosette plant *Lobelia telekii*, Western wallflower

297 *Erysimum capitatum*, Appendix 1: Table S5, and Desert agave *Agave deserti*, Appendix 1:  
298 Table S6). Conger eels serve as an 'exception that proves the rule' because males and females  
299 occupy different ocean depths. Females are obligate semelparous (Appendix 1: Table S4).  
300 Males already live in deep water, so the breeding migration route of males to the deep ocean  
301 is less arduous than in females, and males are apparently iteroparous (Casadevallet al., 2017),  
302 unlike *Anguilla* eels in which both sexes have the same migration distance and show obligate  
303 semelparity (Appendix 1: Table S4, and see below).

304

305 Most semelparous organisms are plants, but published evidence suggests that few plants are  
306 obligately semelparous (Appendix 1: Table S5). One example of a plant that appears to show  
307 obligate death after reproducing once is the desert agave *Agave deserti*, in which the parent  
308 plant mobilises tissue to grow a very large flower stalk. In this species, the floral stalk  
309 exceeds photosynthesis and water transport capacity, and so the adult individual dies soon  
310 after it reproduces. The desert agave appears to follow predictions of the reproductive  
311 investment model, because higher flower stalks may disproportionately increase pollination  
312 and seed set (Appendix 1: Table S6).

313

#### 314 **Pathways to obligate semelparity in males**

315

##### 316 Male pre-copulatory competition and the demographic model

317

318 We find that male animals can achieve obligate semelparity through two distinct pathways.  
319 The first is an adult-biased mortality driver combined with a mechanism of tissue being  
320 depleted through investment in reaching and defending females, female choice, male  
321 competitive searching, or male combat (i.e. pre-copulatory competition), and a sterility

322 mechanism of gonad breakdown after one episode of gametogenesis. Tissue investment in  
323 this context occurs via modes of pre-copulatory and post-copulatory sexual selection  
324 (Appendix 1: Tables S7-S10). A remarkable example is the eel *Anguilla japonica*, which has  
325 an energy-intensive six-month breeding migration of thousands of kilometres in the open  
326 ocean to a specific subtropical deep water spawning ground at seamounts of the Pacific  
327 Mariana Ridge. Breeding migration in this fish is against the prevailing current because  
328 larvae must use passive transport to return to a river on the landmass where the parents lived  
329 as juveniles (Jellyman, 2021). These eels are broadcast spawners that invest most of their  
330 body tissue in migration and in concurrently producing a high volume of gametes  
331 (Tsukamoto et al., 2011). Most of their tissues are depleted by the point of mating, but they  
332 retain fins and enlarged eyes intact when they reach the breeding ground, presumably to  
333 search for mates in the deep ocean. Males spawn with several females in succession  
334 (Tsukamoto et al., 2011). Males must participate in this migration because females do: in  
335 semelparous eels, lampreys, Pacific salmon and (at a smaller scale) the marine isopod  
336 *Paracerceis sculpta* (Shuster, 1991), both sexes participate in simultaneous and energetically  
337 punishing breeding migrations and both sexes are semelparous. For eels, the distance to the  
338 traditional ocean spawning site has increased on an evolutionary time scale, especially for  
339 temperate zone species, as landmasses have moved during the species' 40-70 million years of  
340 evolution (Righton et al. 2012).

341

#### 342 Male post-copulatory competition and the reproductive effort model

343

344 The second pathway to obligate semelparity in males is a driver of post-copulatory  
345 competition resulting from sexual conflict. In this pathway, skewed fitness benefits increase  
346 disproportionately for males that compete via extreme reproductive investment. Males

347 allocate their body reserves of fat, carbohydrate, and protein to gain an advantage in post-  
348 mating competition. The mechanism of death is tissue investment in competitive mate  
349 guarding (spiders and hymenopterans in Appendix 1: Table S8, dasyurid marsupials in  
350 Appendix 1: Table S9), and sometimes sperm production (*Anguilla* spp and the River  
351 lamprey *Lampetra fluviatilis*, Appendix 1: Table S9). Sterility mechanisms associated with  
352 the sexual selection driver of obligate semelparity in males are varied: reproductive organs  
353 are amputated or altered so they become unusable, or testes degrade or cease spermatogenesis  
354 irreversibly before or at maturity, so that all sperm are transferred to a storage location  
355 elsewhere in the body before mating (e.g. several clades of spiders and insects, Appendix 1:  
356 Table S8). Sexual conflict that involves females gaining fitness benefits by escalating male  
357 investment, and the highly skewed nature of male fertilisation success in polygynous and  
358 promiscuous mating systems mean that male reproductive success increases  
359 disproportionately at high levels of reproductive investment, consistent with the reproductive  
360 effort model. In species conforming to predictions of this driver in males, females are not  
361 semelparous. Unlike the demographic model, in which both sexes usually live in the same  
362 habitat so are subject to the same extrinsic pressures, in the reproductive effort model the  
363 driver is not shared in males and females of the same species, so females are not expected to  
364 be semelparous in taxa that show obligate male semelparity.

365

366 An example of male-only obligate semelparity being driven by post-copulatory competition  
367 and sexual conflict is the brown antechinus *Antechinus stuartii* (Appendix 1: Table S9), an  
368 insectivorous dasyurid marsupial. Experimental manipulations show that polyandrous  
369 females of this species benefit from a 'good genes' mechanism of sperm competition. Females  
370 that mate with multiple males have improved offspring survival and lifetime reproductive  
371 success in the wild because the sperm of high-quality males (those with high offspring

372 survival) outcompetes the sperm of poor-quality males. Females escalate post-copulatory  
373 competition among males by compressing and synchronising their one period of sexual  
374 receptivity, extreme promiscuity, and sperm storage before ovulation. Prolonged copulation  
375 (12-14 hours) in brown antechinus is a form of mate-guarding. Escalating circulating stress  
376 hormones during the mating period, then tissue disintegration, internal bleeding, and immune  
377 system collapse soon after mating cause programmed death of all males (Barker et al. 1978).  
378 Three genera in the Family Dasyuridae show obligate semelparity, the other genera in the  
379 Family show a range of male survival rates after mating from facultative semelparity to  
380 iteroparity. Testes size (indicating likelihood of sperm competition; (Pitcher et al. 2005,  
381 Soulsbury 2010) increases with semelparity and is highest in obligate semelparous species  
382 and lowest in species with iteroparous males (Fisher et al. 2013). Male post-mating survival  
383 declines with decreasing mating season duration (Fisher et al. 2013), indicating that intensity  
384 of male competition is associated with male survival.

385

386 Spiders and hymenopteran insects with male obligate semelparity have a similar driver to that  
387 in *Antechinus*: post-copulatory sexual selection with extreme survival costs of sperm  
388 competition and mate-guarding. Several authors have attributed the ultimate cause of male  
389 spider semelparity to adult mortality risk (Fig. 1) with a long interval between breeding  
390 opportunities (Appendix 1: Table S8), but have not quantified this risk in the wild or obtained  
391 juvenile survival estimates. We suggest that spiders with male-only semelparity conform to  
392 predictions of the reproductive effort model and no age-specific mortality driver is needed to  
393 evolve reproductive death in males. The demonstration by Fromhage et al. (2005) that  
394 selection for male semelparity via sexual cannibalism in spiders does not need high search  
395 costs (*i.e.*, low survival between reproductive episodes) supports our suggestion. Fromhage et  
396 al. (2005) point out that the argument that small males are unlikely to find another female

397 after one mating is inconsistent with the intense sexual competition and adaptations  
398 associated with defence of paternity in males of these species.  
399  
400 Species that have obligate semelparity only in males but not in females, such as some spiders,  
401 hymenopteran insects and dasyurids, show remarkable convergence in one peculiar  
402 reproductive trait: in all these species where data are reported, males severely limit their  
403 sperm supply immediately before sexual maturity, well before their only chance to mate. For  
404 example, in the comb-footed spider *Tidarren* spp, males amputate one pedipalp at their  
405 penultimate moult just before sexual maturity (Knoflach and Van Harten 2000). In the orb-  
406 weaver *Nephila clavipes*, testes cease producing sperm before maturity, and all sperm are  
407 transferred to the pedipalps (Michalik and Rittschof 2011). In social insects including  
408 honeybees and queenless ants *Dinoponera quadriceps*, spermatogenesis ceases during the  
409 pupal stage before maturity (Appendix 1: Table S8). Male *Antechinus* and *Phascogale* cease  
410 spermatogenesis just before maturity, a month before mating, and store their lifetime supply  
411 of sperm in the epididymus while their sperm-producing tissue deteriorates (Appendix 1:  
412 Table S10).  
413  
414 Limiting ability to transfer sperm is especially puzzling in animals that have only one  
415 reproductive opportunity. Authors have given species-specific reasons. For instance, in the  
416 tangle-web spiders *Tidarren* spp., that emasculation improves endurance during competitive  
417 searching and mobility in contests on the female's web, or accelerates male maturity giving  
418 males more time to find a female (Knoflach and van Harten, 2000, 2001; Knoflach and  
419 Benjamin, 2003; Ramoset al., 2004). In the golden silk orb-weaver spider *Nephila* and the  
420 dasyurid *Antechinus*, that males improve endurance for mate-guarding by diverting energy  
421 from testes to muscles and other tissue (Christenson et al., 1985; Cohn and Christensen,

422 1987, 1988; Michalik and Rittschof, 2011; Fisher et al. 2013). However, it is striking that  
423 such diverse taxa that all show male-only semelparity all have pre-breeding mechanisms to  
424 curtail the ability to transfer sperm. We propose a new hypothesis- loss of future reproductive  
425 capacity in obligate semelparous male animals is analagous to capital breeding in female  
426 animals (Drent and Daan 1980; Jonsson 1997). Capital breeders can accumulate and rapidly  
427 transfer a much larger store of energy and other resources for a reproductive bout than  
428 income breeders can. 'Capital breeding' obligate semelparous males can transfer a large  
429 amount of sperm at once. Other male animals are 'income breeders' that continue to replenish  
430 sperm supplies during their reproductive life, but have lower maximum rates and amounts of  
431 sperm transfer per copulation. This strategy is similar to income breeding females, which  
432 transfer energy to developing offspring at a lower rate for longer than capital breeders do. We  
433 propose that pre-breeding loss of future reproductive capacity is associated with intense post-  
434 mating sexual competition. Rather than replenishing sperm gradually and progressively  
435 transporting it outside his body, a semelparous male keeps his lifetime store of sperm in one  
436 location near the outside of his body to transfer quickly at the crucial time for competition.

437

438 We propose that the reproductive effort driver of obligate male semelparity applies to  
439 *Antechinus*, spiders, and hymenopteran insects that have a mechanism of sexual selection  
440 involving costly somatic damage. Extreme costs to males can evolve when there is  
441 competition between males to prevent further matings by rival males in the form of tissue-  
442 depleting mate guarding, combined with high benefits to females if they promote polyandry.  
443 An example of this cost is the mating plug of honeybees and some ants, which has become so  
444 complex and difficult for females to remove that disengaging involves the female tearing or  
445 cutting off part of the male's abdomen (Baer, 2005; Monnin, 1998).

446

447 Unlike post-mating guarding, fertilisation success through pre-mating male conflict (fighting  
448 and competitive searching) is unlikely to increase disproportionately at lethally high levels of  
449 body reserve investment. This relationship may explain why we found no evidence that pre-  
450 mating sexual selection is associated with obligate semelparity in males (Appendix 1: Tables  
451 S7-10).

452

453 Why are there are no semelparous males in plants?

454

455 We suspect that only animals show obligate semelparity in males. We found no published  
456 evidence of the existence of dioecious plants with semelparous males. Semelparity in males  
457 is driven by sexual selection, which does occur in plants (Delph and Ashman 2006). Sexual  
458 selection in plants can include competition between pollen grains via transport speed,  
459 fertilisation compatibility and precedence, attraction of pollinators in a flower, or interactions  
460 on the body of a pollinating insect (Lankinen et al. 2017, Minnaar et al. 2019). Unlike the  
461 more violent modes of sexual competition possible in some male animals (Appendix 1: Table  
462 S8), none of these mechanisms can increase the competitiveness of an individual male  
463 function by killing the parent plant. There is no equivalent of sexual conflict-driven costly  
464 mate-guarding in male plants. There is no sexual selection mechanism in plants that can  
465 increase fertilisation success via somatic damage only in males, even in wind or water-  
466 pollinated plants, which have high pollen volume. In insect-pollinated plants, investment in a  
467 large volume of pollen at once is not adaptive for males. In monoecious plants, fitness returns  
468 from the male function but not the female function level off with increasing expenditure  
469 (DeJong and Klinkhamer 1989) and there are diminishing returns if insects carry large pollen  
470 loads (Minnaar et al. 2019). High investment in pollen is likely to have a low survival cost  
471 regardless of pollination mode, and the low cost of the male function can be important in

472 plant life history evolution: some plants change sex according to environmental conditions on  
473 a schedule driven by the relatively higher costs involved in ovule production than in pollen  
474 production (Bierzychudek 1982).

475

476 It is also possible that a mechanism of costly male competition has evolved in plants and the  
477 apparent lack of male-only semelparity in the Plant Kingdom is due to our sparse knowledge  
478 of plant diversity (Allen 2003), especially regarding the sex-specific demographic  
479 performance of plants (but see Petry et al. 2016, Römer et al. 2022). However the majority of  
480 the Plant Kingdom is characterised by reproductive arrangements other than dioecy, and  
481 hermaphroditism and other sexual arrangements are common (Bernard et al. 2022). Perhaps  
482 because annuals risk reproductive failure in their only reproductive episode if pollination  
483 fails, most annual plants are monoecious and capable of self-fertilization, and dioecy is more  
484 common in iteroparous than in semelparous plants (Friedman 2020).

485

#### 486 Semelparity in small mammals

487

488 Dasyurid marsupials in the genera *Antechinus*, *Phascogale*, and *Dasykaluta* are often  
489 considered to be the only semelparous terrestrial vertebrates (e.g. Kern and Gems 2022).  
490 However, there are several published investigations of semelparity in other small mammals  
491 including both male and female rodents and didelphid marsupials. Female examples include  
492 the Death Valley population of the desert woodrat *Neotoma lepida*, which is semelparous in  
493 hot years because the large body size that maximises fecundity is lethal in summer, and  
494 persistence at a smaller size would not achieve the same lifetime reproductive output over  
495 two seasons (Smith and Charnov 2001). Male examples include Arctic ground squirrels  
496 *Urocitellus parryii*. Males of this species show a programmed rise in stress hormones during

497 their three-week high-latitude summer breeding season, they lose weight, and intense pre-  
498 mating competition kills around half of the males during the mating period (Boonstra et al.  
499 2001, Edwards et al. 2016). The driver of this extreme outcome appears to be escalating  
500 reproductive competition due to a single concentrated breeding period separated by a long  
501 interval to the next possible reproductive opportunity. Male Arctic ground squirrels thus  
502 appear to have a similar driver and mechanism to facultatively semelparous male dasyurids,  
503 such as dibblers *Parantechinus apicalis*, although a lower male death rates (Mills and  
504 Bencini 2000).

505

506 Female semelparity occurs in some other small marsupial clades. For example, the wongai  
507 ningai *Ningai ridei* is an 8g species of the semi-arid zone that breeds seasonally, has a one-  
508 year lifespan and is capable of rearing two litters in its single breeding season in captivity, but  
509 apparently never does so in the wild (Fisher et al. 2013). The dasyurid genus *Sminthopsis*  
510 includes some species with females that can only raise a single litter a year and rarely survive  
511 two years, for example the grey-bellied dunnart *S. griseoventer* (Fisher et al. 2013). This  
512 genus also includes many species with iteroparous females (Collett et al. 2018). Because  
513 trapping and museum records show that adult males and females are absent in part of the year  
514 and males show signs of stress, some small insectivorous South American didelphid  
515 marsupials are often claimed to have the same life history strategy of facultative semelparity  
516 as Arctic ground squirrels and dibblers (the dasyurid *Parantechinus apicalis*) (Appendix 1:  
517 Table S9). Examples include the forest and grassland-dwelling mouse opossums  
518 *Gracilinanus agilis*, *G. microtarsus*, *Marmosops incana*, *M. paulensis*, and *Monodelphis*  
519 *dimidiata* (Pine 1994, Martins et al. 2006, Leiner et al. 2008, Lopes and Leiner 2015).  
520 However, field studies on the gracile agile mouse opossum *G. agilis* showed that the mating  
521 period was split into two times of year, births were not strongly synchronised, and death did

522 not occur soon after reproduction (Martins et al. 2006, Lopesa and Leiner 2015). Males had  
523 low survival three months after the July mating period, and females had low survival 4-5  
524 months after birth of young (Martins et al. 2006, Lopesa and Leiner 2015). Although males  
525 showed fur loss and lose weight during the breeding season, the long delay after mating until  
526 male deaths and the repeated or protracted periods of female receptivity suggest that intense  
527 sexual competition with a long interval between breeding seasons is not the driver, and the  
528 mechanism of male death does not appear to be lethal investment in mate guarding escalated  
529 by sexual conflict. The drivers and mechanisms of the high male death rate are unclear in  
530 didelphids.

531

#### 532 Trade-offs and plasticity in semelparous organisms

533

534 Variation in post-reproductive survival can occur in semelparous species as a result of trade-  
535 offs between allocation to reproduction versus maintenance. Female salmon that arrive first at  
536 the spawning site can defend the best nest locations, but must defend them for longer after  
537 breeding to prevent egg mortality that would ensue if subsequent females were to take over  
538 the nest. Early-arriving females restrain investment of fat reserves in eggs, which decreases  
539 fecundity, and instead they allocate body reserves to guarding longer (Hendry et al. 2004).  
540 Male antechinus that invest the most in sperm competition die first, which may also mean a  
541 trade-off between sperm production and mate guarding duration in the wild (Fisher and  
542 Cockburn 2006).

543

#### 544 Energy constraints and trophic level

545

546 Semelparity is not a viable strategy for organisms that are constrained to have few offspring  
547 per reproductive bout. Clearly, for a strategy to be viable in the long term, adult individuals  
548 must replace themselves, allowing for juvenile mortality. This rationale is a suggested reason  
549 for why there are no semelparous birds, as flight energetics precludes high enough allocation  
550 to one clutch (Braithwaite and Lee 1979). In marsupials, evolutionary changes in  
551 reproductive output have been constrained by diet quality, so only carnivorous, insectivorous,  
552 or nectarivorous species have large litters (Fisher et al. 2001). Such a dietary energy  
553 constraint on fecundity might apply more broadly to males and to other clades. We suggest  
554 that trophic level may constrain the evolution of semelparity. Ninety-three percent of the  
555 animal species and clades that we have identified in this review as semelparous are predators.  
556 The exceptions are the herbivorous desert woodrat *Neotoma lepida*, the frugivorous insect  
557 *Parastrachia japonensis*, the algae-eating fish the ayu *Plecoglossus altivelis*, the herbivorous  
558 isopod crustacean *Hemilepistus reaumurii*, granivorous male harvester ants *Pogonomyrmex*  
559 spp, and herbivorous male Arctic ground squirrel *Urocitellus parryii*, which are all  
560 facultatively semelparous.

561

562 Whether or not an organism shows indeterminate growth (individuals continue to grow after  
563 maturity) may also influence selection on semelparity. This is so because both females and  
564 males of continually-growing organisms typically have size-dependent fecundity and  
565 reproductive success (Rees et al. 2014). In species with indeterminate growth, factors that  
566 reduce growth rate and thus limit offspring number, such as poor territory quality, could  
567 inhibit facultative semelparity (Iguchi and Tsukamoto 2001).

568

569 Extreme environments such as hot, dry deserts or high-latitude cold ocean depths constrain  
570 the rate of tissue growth through food or water scarcity and metabolic constraints. Many

571 semelparous organisms in these environments reach sexual maturity after years or decades in  
572 the juvenile phase (Young and Augspurger 1991, Robison et al. 2014). However,  
573 phylogenetic comparisons do not support a constraint linked to the evolution of semelparity  
574 to explain extended immaturity evolves in plants, because iteroparous relatives of long-lived  
575 semelparous plants have similar long juvenile stages (Young and Augspurger 1991).

576

577 Pathways out of semelparity- can obligate reproductive death be reversed?

578

579 Williams, quoted in Stearns (1976), suspected that once obligate semelparity has evolved it  
580 ought to be irreversible. This suspicion has proved to be incorrect: obligate semelparity is  
581 reversible. The biological mechanisms to reverse semelparity are in fact straightforward. In  
582 animals, one evolutionary pathway out of obligate semelparity for animal species that have  
583 lost the capacity to pause reproduction seasonally and regenerate their gonads more than once  
584 is to split the gametes from their one cycle of gametogenesis into a series of batches.

585 Semelparous females that have lost the ability to ovulate more than once can split their one  
586 clutch into multiple spawning events (Grearson et al. 2021), and males that have lost the  
587 ability to produce more than one batch of sperm because their testes cannot regenerate can  
588 allocate their finite store of sperm to a series of matings. For example, golden orb-web  
589 spiders *Nephila senegalensis* have reversed genital damage behaviour and sexual  
590 cannibalism, which occur in other species in the clade, but spermatogenesis still ceases with  
591 maturation. This species re-evolved iteroparity in males by partitioning the sperm supply on  
592 their two pedipalps between up to four females (Schneider and Michalik 2011).

593

594 Such reversals have happened multiple times in octopus and squid. Cephalopods have an  
595 optic gland that has similar function to the vertebrate pituitary. In females, the mechanism of

596 brooding behaviour and tissue disintegration associated with semelparity depends on  
597 secretion of hormones by this gland (Wang and Ragsdale 2018). Optic gland removal causes  
598 both sexes to resume feeding and live a few months longer, but not breed again (Wodinsky  
599 1977). Female octopus cannot regenerate their ovaries. However, although the ancestors of  
600 the ovoviparous two-spot octopus *Octopus chierchiae* were semelparous (Grearson et al.  
601 2021, Ibanez et al. 2021), this species splits a single clutch of oocytes into batches that  
602 mature at different times, and distribute these across a spawning period (Grearson et al.  
603 2021). In octopus (Superorder Octopodiformes in the subclass Coleoidea), most species show  
604 obligate semelparity, and such clutch-splitting appears to have evolved in two tropical clades  
605 during the Cenozoic (Ibanez et al. 2021). Most species of the diverse, globally distributed  
606 Superorder Decapodiformes (squids and sepiids) evolved from clutch-splitting  
607 ('asynchronous ovulating') ancestors in a separate clade from that of ancestral  
608 Octopodiformes, and most squid retain the strategy of multiple spawning in their single  
609 breeding season (Ibanez et al. 2021). Fisheries data suggest that both sexes in the Japanese  
610 firefly squid *Watasenia scintillans* are obligate semelparous. Males die a month before  
611 females spawn, and most females in the reproductive period contain the stored spermatophore  
612 of only one male (Sato et al. 2020). Other species in the Family Enoploteuthidae are  
613 asynchronous ovulators (Ibanez et al. 2021), so obligate semelparity appears to have been  
614 regained by firefly squid. Unfortunately, we know little about the natural history of this  
615 pelagic species.

616

#### 617 Data gaps and modelling opportunities

618

619 Some drivers and mechanisms suggested by mathematical models or evolutionary ecology  
620 studies have not been demonstrated conclusively in any organism. One of these drivers is

621 intraspecific exploitation competition in which juveniles disproportionately reduce the  
622 survival of adults. Semelparity is associated with high intraspecific exploitation competition,  
623 especially if births are synchronous and offspring cannot disperse (Acker et al. 2014). Such a  
624 mechanism has been proposed in plants when seedlings compete with parents (Silvertown  
625 1983). Edeline (2016) proposed that the cause of facultative semelparity in a typically  
626 iteroparous fish was intraspecific competition. A population of Japanese rice fish *Oryzias*  
627 *latipes* confined to a ditch with scarce prey (zooplankton) showed complete adult mortality  
628 over two to five weeks. Females invested heavily in reproduction and lost mass. Edeline  
629 (2016) interpreted these data to show that asymmetric intraspecific food competition from  
630 juveniles entirely eliminated the adults. However, this research was not an experimental  
631 study.

632

633 The idea that adult death evolves to benefit juveniles has been put forward many times, for  
634 example (Diamond 1982) suggested that male antechinus sacrifice themselves to save  
635 juveniles from competition at a population level [an idea refuted by Fisher and colleagues  
636 (Fisher et al. 2006, Fisher et al. 2013) who demonstrated individual sexual selection in  
637 antechinus, not population-level group selection]. Many bamboo species are semelparous and  
638 reproduce in synchrony so that dense stands die *en mass*. Nicholson (1922) hypothesised that  
639 this strategy is adaptive because it diminishes competition for light for the new cohort.  
640 However, while it may explain why the strategy is sustainable, this hypothesis does not  
641 explain how semelparity in bamboos evolved in terms of individual fitness. Janzen (1976)  
642 suggested that to increase the survival of their offspring through higher light availability,  
643 adult bamboos could drop their leaves (of which they are capable) and survive on starch  
644 reserves instead of dying. Further, there is evidence that the strategy is facultative: applying  
645 fertiliser to some normally semelparous bamboo species can result in iteroparity (Janzen

646 1976). The reasons why semelparous bamboos have such a complex life cycle remain poorly  
647 understood.

648

649 The second of these drivers is size-specific predation. Iguchi and Tsukamoto (2001)  
650 suggested that predation by birds may be a driver of high adult mortality specifically in large  
651 individual ayu fish, and the reason why large female fish allocated up to 30% of body mass to  
652 a single spawning event that depleted their body reserves, whereas small individuals  
653 continued to accrue protein and fat to spawn twice, however no evidence of size-specific  
654 predation was presented.

655

656 Many studies that investigate the evolution of semelparity in one sex do not provide  
657 information on the other sex, and many invertebrate taxa are reported to have semelparous  
658 species but no hypothesis has been suggested or predictions tested. These species include  
659 polychaetes in the family Nereidae (Finch 1994), the freshwater leech *Erpobdella octoculata*,  
660 which is apparently iteroparous in some lakes and semelparous in others (Maltby and Calow  
661 1986), spiders in the genus *Seothyra*, the planarian *Dendrocoelum lacteum* and other sucker-  
662 bearing flatworms in the freshwater Triclad Family Dendrocoelidae (Woolthead and Calow  
663 1979, Calow and Read 1986), the desert isopod crustacean *Hemilepistus reaumurii* (Ayari et  
664 al. 2021), and some cohorts of the sea squirt *Botryllus schlosseri* (Grosberg 1988). In the  
665 insectivorous midge *Bezzia modocensis* and others in the Dipteran tribes Heteromyiini,  
666 Sphaeromyiini, and Palpomyiini, the female eats the male by piercing his head during mating  
667 in flight and a torn-off terminal segment remains attached to her in the mating position  
668 (Downes 1978); behaviour reminiscent of the mate-guarding mechanism of semelparity in  
669 some male Hymenoptera. However, there have been no investigations of adaptive  
670 semelparity in these flies. Around 1% of fish are semelparous according to Finch and Rose

671 (1995). There being *ca.* 32,000 species of fish (Mora et al. 2011), this implies that more than  
672 3,200 species have unstudied drivers and mechanisms of semelparity.

673

674 Plants may be more likely to evolve semelparous life history strategies than animals because  
675 the plant bauplan, consisting of shoot apical meristems that can continue to grow *or* set to  
676 flower (but not both) results in many iteroparous populations having some individuals with  
677 high reproductive effort at the cost of survival (Metcalf et al. 2003). Semelparity in plants  
678 includes annuals and perennials. Of the >390,900 plant species known, 6-10% are annual  
679 species (Byng et al. 2016, Poppenwimer et al. 2022).

680

681 Annual plants complete their life cycle in less than a year and have a single reproductive  
682 event. Population models based on the premise that annuals would risk death without  
683 reproduction if they delayed flowering have been very successful at predicting plant size at  
684 reproduction, suggesting that the demographic model of semelparity applies broadly to  
685 annual plants (Metcalf et al. 2003). A widely recognised but unknown proportion of the plant  
686 Kingdom are facultative annual or biennial species. These are annual plant species that can  
687 postpone their single reproductive event, and thus death, until their second year. Drivers of  
688 facultative annual life history evolution in plants are unknown but probably involve aspects  
689 of environmental quality and predictability (Friedman 2020). More than 100 plant Families in  
690 30 orders of angiosperms have independently evolved an annual life history strategy from a  
691 perennial ancestor (Stebbins 1950, Soltis et al. 2013). Semelparous (monocarpic- a synonym  
692 applied to plants) perennial plants live for more than a year before their single reproductive  
693 event. A relatively small proportion of perennial plants are semelparous. Perennial  
694 semelparity is scattered across the phylogeny of plants and includes >30 Families (Young and  
695 Augspurger 1991, Metcalf et al. 2003).

696

697 Distinctions between semelparity, terminal investment, and senescence

698

699 Terminal investment is defined as an increase in reproductive effort near the end of life, and  
700 involves an adaptive trade-off that produces fitness benefits such as improved offspring  
701 survival and growth (Williams 1966). Triggers for terminal investment indicate a high chance  
702 of impending death, and can include age, nutritional status, infection, or temperature  
703 (Duffield et al. 2017). Terminal investment is distinct from senescence. Senescence is the  
704 post-maturity decline of organismal vitality with age that reflects non-adaptive constraints  
705 resulting from genetic antagonistic effects acting early versus late in life (Williams 1957),  
706 accumulation of deleterious mutations through time (Medawar 1952), or inefficient trade-offs  
707 in the allocation of limiting resources to maintenance versus reproduction (Kirkwood 1977).  
708 Senescence is much more common than terminal investment, although senescence is not  
709 universal (Roper et al. 2021). Except in situations of cooperative family or grandparental care  
710 (Pavard et al. 2008), senescence is not adaptive. In contrast, reproductive death can be  
711 favoured by natural selection (Ronce and Promislow 2010). Indeed, lethal allocation to  
712 reproduction that results in semelparity appears to be a form of terminal investment rather  
713 than a form of senescence.

714

715 Programmed death, sometimes also confusingly termed senescence (Salguero-Gomez et al.  
716 2013), is also distinct from semelparity. Programmed death is not necessarily reproductive  
717 death, and it can be adaptive without terminal investment or semelparity. For example,  
718 mayflies are short-lived insects in the Order Ephemeroptera (~3000 species). Adult mayflies  
719 show programmed death because they have no mouthparts or functioning gut (Finch and  
720 Rose 1995). Mayflies have an aquatic nymph stage for several months or years, then two

721 instars out of water. The final instar when they are sexually mature lasts only days. However,  
722 females mate and lay successive clutches throughout adult life, they do not show  
723 reproductive death, and they are not semelparous (Clifford 1982). Adult periodical cicadas  
724 *Magicada* spp. also lack a gut and mouthparts at maturity and show a similar strategy to  
725 mayflies in having a long nymph stage and brief adult life in which they produce multiple  
726 clutches and have no mouthparts, although it is sometimes claimed that they are semelparous  
727 (Bell 1980, Finch 1994).

728

729 Adaptation to adult-biased mortality: early maturity versus semelparity

730

731 High adult mortality relative to juvenile mortality often selects for early sexual maturity  
732 rather than for semelparity. Age at maturity typically trades off with offspring number and  
733 growth along the slow-fast continuum (Fisher et al. 2001, Salguero-Gomez et al. 2016, Paniw  
734 et al. 2018). However, age at maturity does not necessarily trade-off with parity: semelparous  
735 animals and plants can mature quickly (crab spiders, wild beet, squid) or remarkably slowly  
736 (*Anguilla* eels, agave). In recent decades, several studies that have evaluated trade-offs  
737 between investment in reproduction, survival, and development have concluded that the  
738 degree of semelparity is a major axis of life history variation (Dunham and Miles 1985,  
739 Gaillard et al. 1989, Salguero-Gomez et al. 2016, Healy et al. 2019). In other words, a  
740 species' position on the fast-slow continuum is not dependent on position on the semelparity-  
741 iteroparity axis.

742

743 An example of fast life history occurring without semelparity is found in the smallest fish,  
744 which are subject to high mortality from extrinsic causes and have evolved fast and  
745 iteroparous life history strategies. African turquoise killifish *Nothobranchius furzeri* have

746 extremely high adult mortality rates because they exploit temporary rain puddles to breed.  
747 Adults breed continually from two weeks old before succumbing to mutation load  
748 mechanisms of senescence at ten weeks old (Cui et al. 2019, Reichard and Polacik 2019).  
749 Amazonian floodplain stream-dwelling electric knifefish *Brachyhypopomus* spp are also  
750 iteroparous in a short season and show terminal investment as their seasonally-present habitat  
751 evaporates (Waddell and Crampton 2022). The adorned dwarf goby *Eviota sigillata* is a tiny  
752 reef fish with an eight-week lifespan. Males fan and guard eggs, increasing offspring  
753 survival, and adults have an extreme daily mortality of 8%, mainly due to predation. This  
754 fish's adult lifespan is ~25 days, and it produces three clutches (Depczynski and Bellwood  
755 2006). Experiments show that Trinidadian guppies in streams with more intense predation on  
756 adults evolve early maturity and have larger broods and higher reproductive rates (Reznick et  
757 al. 2006). In commercial marine fisheries, fishing pressure targets large adults, and severe  
758 over-fishing has also selected for earlier maturity in cod and whales in only a few generations  
759 (Olsen et al. 2004, Clements et al. 2017).

760

761 Rather than favouring semelparity, recent dramatic increase in adult mortality has selected for  
762 early maturity in female Tasmanian devils *Sarcophilus harrisii* (Lachish et al. 2009, Lazenby  
763 et al. 2018). This mammal species has a single annual breeding season, so selection might be  
764 expected to favour high reproductive effort if females are unlikely to survive to raise a litter  
765 the following year. It is also possible that that the selection for early maturity could be the  
766 first step towards a future annual semelparous strategy (Fig 1). However, currently it seems  
767 that a sharp increase in mortality after the first mating season has failed to trigger terminal  
768 investment. The novel fatal Devil Facial Tumor Disease (DFTD) is an infectious cancer that  
769 was first recorded in 1996 and has caused a mean 32% decline in the global population of this  
770 dasyurid marsupial, and local declines of >80% (Cunningham et al. 2021). This disease is

771 transmitted by facial biting, which adults frequently do during the single annual mating  
772 period. Females typically matured at two years old prior to this disease. Lachish (2009) found  
773 that the incidence of females breeding as one-year olds (which were rarely infected)  
774 increased progressively from ~5% to >50% in five years after DFTD. Lazenby et. al (2018)  
775 confirmed that selection for early breeding has continued, but because DFTD is spread by  
776 breeding behaviour and one-year olds now breed, incidence in one-year olds has increased to  
777 ~40% in the last 25 years.

778

779 Lachish (2009) suggested that capacity for reproductive effort is constrained in female  
780 Tasmanian devils because litter size is set by teat number not ovulation. Tasmanian devils  
781 give birth to up to 30 supernumary neonates and there are only four teats in the pouch.  
782 However, in females of another similarly constrained monoestrous dasyurid with  
783 supernumary young, the brown antechinus, terminal investment increases growth and  
784 survival of young in a full pouch at the expense of maternal body reserves and post-breeding  
785 survival (Fisher and Blomberg 2011). In contrast to the strong adaptive response of declining  
786 age at maturity, Lazenby et. al (2018) found no progressive increase in Tasmanian devil  
787 offspring survival since DFTD arose. Release from intraspecific competition after the sharp  
788 decline in population density resulted in higher growth rate in one-year old Tasmanian devils,  
789 allowing early reproduction, rather than resulting in greater investment in offspring growth  
790 and survival (Lachish 2009).

791

792 Why is obligate semelparity rare?

793

794 In animals, a decrease in adult mortality can induce an increase in age at maturity in a short  
795 time. For example, in red deer *Cervus elaphus* released from the extrinsic pressure of culling,

796 mean age at first breeding shifted to an older age class almost immediately, although adult  
797 survival did not change for twenty years (Coulson et al. 2004). Our compiled data indicate  
798 that much the same extrinsic causes of mortality operate in adults before, during, and after  
799 their first reproductive event (Appendix 1: Tables 1-10), yet semelparity and terminal  
800 investment remain rare responses to high adult mortality in the short term. One reason may  
801 be that the extent of natural variation in age at maturity in populations is higher than the  
802 extent of variation in allocation to gametes. The level of investment associated with obligate  
803 semelparity is unlikely to exist in any individuals of an iteroparous population. For example,  
804 in Tasmanian devils, before DFTD, although females were iteroparous, 5% of the female  
805 population nonetheless bred at one year old (Lazenby et. al 2018). However, because obligate  
806 semelparity is an extreme of the iteroparity-semelparity life history axis, it appears less likely  
807 that in populations of the iteroparous ancestor of *Anguilla* eels some individuals were  
808 routinely semelparous through lethal investment their skeletal, muscle, and gut tissue in  
809 gametes to enhance fecundity. The evolutionary change to extreme reproductive allocation  
810 associated with obligate semelparity and reproductive death would thus be slower than the  
811 evolutionary change to universal early breeding.

812

813 Semelparity is common in plants but obligate semelparity appears to be rare. Plant meristems  
814 are semelparous because growth stops when the floral induction pathway is activated. Thus,  
815 the evolution of semelparity from an iteroparous ancestor should be straightforward in plants  
816 because of the ease of transfer from somatic to reproductive tissue (Silvertown 1996). We  
817 suggest that this ease of tissue transfer and mode of growth also means that the evolution of a  
818 mechanism at maturity to prevent future reproductive capacity is less likely in plants than in  
819 animals.

820

## 821 **Conclusions**

822

823 Theoretical frameworks to explain the evolution of semelparity are based on the premise of a  
824 survival cost of reproduction. These frameworks emphasize either a high mortality risk after  
825 the first reproductive event for environmental reasons (the demographic model), or  
826 disproportionate fitness benefits at higher reproductive effort (the reproductive effort model).  
827 Our extensive review of published evidence shows that most semelparous animal and plant  
828 species follow predictions of the demographic model. High adult mortality risk after breeding  
829 is the result of onerous breeding migrations at maturity, predation or parasitism by specialist  
830 natural enemies that target adults, climate extremes that harm large and mature individuals, or  
831 the constraint of food or pollinators needed for successful reproduction only being available  
832 in a short season when adults are very unlikely to survive the interval to the next reproductive  
833 season under these risks.

834

835 We suggest that there are multiple pathways to sex-biased semelparity. In females,  
836 mechanisms that deplete body tissue to increase reproductive output are adaptive when future  
837 reproduction is precluded by one of these environmental drivers of adult-biased mortality  
838 risk. The fact that nearly all known animal species with semelparous females are predators  
839 with high-energy diets (e.g. spiders, cephalopods, eels, lampreys, salmonids) suggests an  
840 energy constraint to the ability to increase reproductive output by depleting body stores  
841 sufficiently to compensate for only breeding once. In species in which both sexes are  
842 semelparous, the sexes share an environment of high post-breeding mortality risk.

843

844 In animals in which only males are semelparous (e.g. antechinus, some spiders, bees), the  
845 driver is post-mating sexual competition between males exacerbated by sexual conflict

846 (Fisher et al. 2013, Schwartz et al. 2016). Females escalate post-mating competition to gain  
847 fitness benefits from sperm competition or cryptic female choice (Fisher et al. 2006). In this  
848 way, males can increase their reproductive success through a mechanism of competition that  
849 causes somatic damage. We suggest that this phenomenon is a mechanism of mate-guarding,  
850 such as amputating a critical body part to serve as a mating plug, using their whole body as a  
851 mating plug, inciting sexual cannibalism that delays further mating by the female, or  
852 depleting their energy stores and catabolising muscle and skin to fuel continuous activity with  
853 repeated, prolonged copulations. In organisms with obligate male-only semelparity, the  
854 mechanism of death is decoupled from the mechanism of reproductive capacity loss. This  
855 mechanism often occurs at sexual maturity, when spermatogenesis ability ceases or the male  
856 amputates a reproductive appendage. We propose that this pre-breeding loss of future  
857 reproductive capacity is associated with a male post-mating sexual competition strategy  
858 analogous to 'capital breeding' (Jonsson 1997), in which rather than replenishing sperm  
859 gradually and progressively transporting it to the outside of his body (the 'income breeding'  
860 strategy of most male organisms), a semelparous male keeps his lifetime store of sperm in  
861 one location near the outside of his body to transfer quickly in his single mating or  
862 concentrated consecutive matings. Male-only semelparity is absent in plants because plants  
863 lack a mechanism of sexual selection that could advantage males through somatic damage.  
864 High adult mortality risk is not a condition of the evolution of male-only semelparity, which  
865 is consistent with the reproductive effort model.

866

867 Understanding why males and females of particular taxa have evolved obligate semelparity  
868 can help us to predict survival of harvested and threatened species under pressure from  
869 climate change, drought, predators, and diseases that kill adults. For example, increasing  
870 aridity can select for semelparity in short-lived plants through a mechanism of adult-biased

871 mortality due to heat and water stress, but other consequences of climate change can also  
872 disadvantage short-lived semelparous plants and birds (Jiguet et al. 2007, Tuljapurkar et al.  
873 2009, Paniw et al. 2018). Harvesting typically targets adults (Olsen et al. 2004, Traill et al.  
874 2014, Clements et al. 2017). Because the demographic model largely explains the evolution  
875 of semelparity in these groups, human pressures on adults are likely to favour evolutionary  
876 transitions towards annualization and thus potentially forced semelparity in many plants,  
877 female animals, and animals in which both sexes share environmental risks as adults.

878

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880

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884

885

### 886 **Author Contributions**

887

888 D. Fisher and R. Salguero-Gomez collated the publications, extracted information, contributed  
889 ideas and co-wrote the manuscript.

890

891

### 892 **Conflict of Interest Statement**

893

894 We declare no conflicts of interest.

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1374 **Figure captions**

1375

1376 Figure 1. The demographic model hypothesis to explain the evolution of semelparity. The  
1377 demographic model predicts that semelparity will be favoured when adult post-breeding  
1378 mortality risk is high relative to juvenile mortality risk. Increases in future mortality can  
1379 select for a semelparous life history strategy. A) A hypothetical age-specific reproductive  
1380 schedule (orange, solid line) of an ancestral iteroparous species where, passed the age at  
1381 maturity ( $L_{\alpha}$ ), multiple reproductive events occur during the lifespan of the organism. In this  
1382 species, the mortality risk schedule (blue, solid line) is not accentuated. B) If the risk of  
1383 mortality increases strongly at advanced ages, the reproductive window will become right-  
1384 truncated, narrower, and will ultimately lead to a semelparous life history strategy. Note that  
1385 the age at first reproduction can also shift to earlier ages in this scenario (Coulson et al.,  
1386 2004; Reznick et al. 2006).

1387

1388 Figure 2. The reproductive effort model hypothesis to explain the evolution of semelparity.  
1389 The reproductive effort model predicts that semelparity is adaptive when fitness benefits of  
1390 reproduction increase disproportionately at high levels of reproductive effort, or if a survival  
1391 cost of reproduction has most effect at low reproductive effort. Semelparity evolves when  
1392 reproductive effort is outweighed by the reproductive success in a single reproductive event.  
1393 This relationship is captured by the relationship between A) reproductive effort and  
1394 reproductive success, or B) reproductive effort and reproductive success normalised by unit  
1395 of reproductive success. Modified from Young (1990).

1396

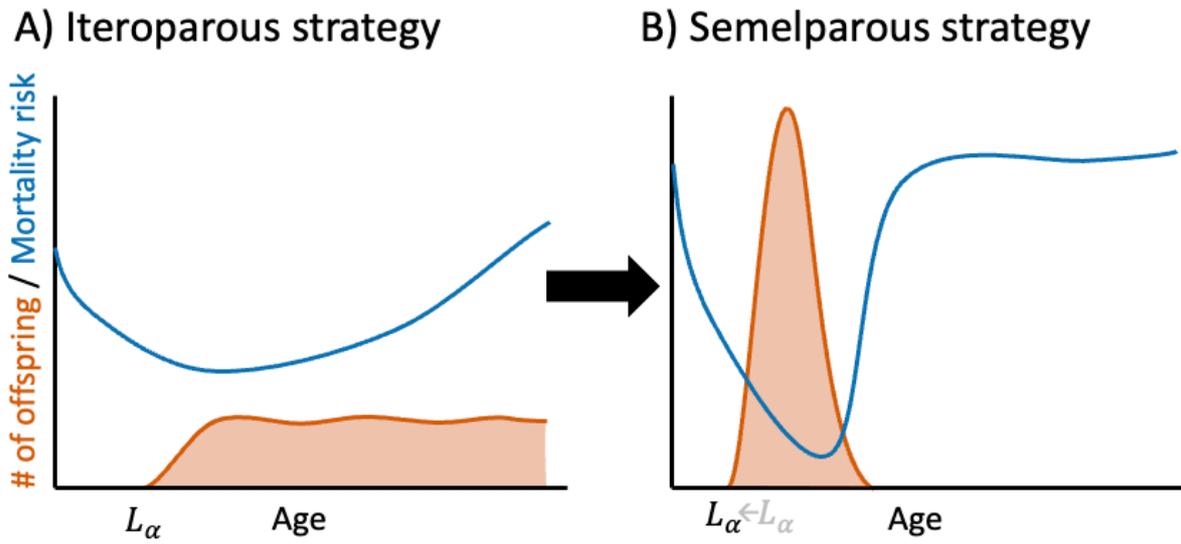
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1398 **Figures**

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1400 **Figure 1**

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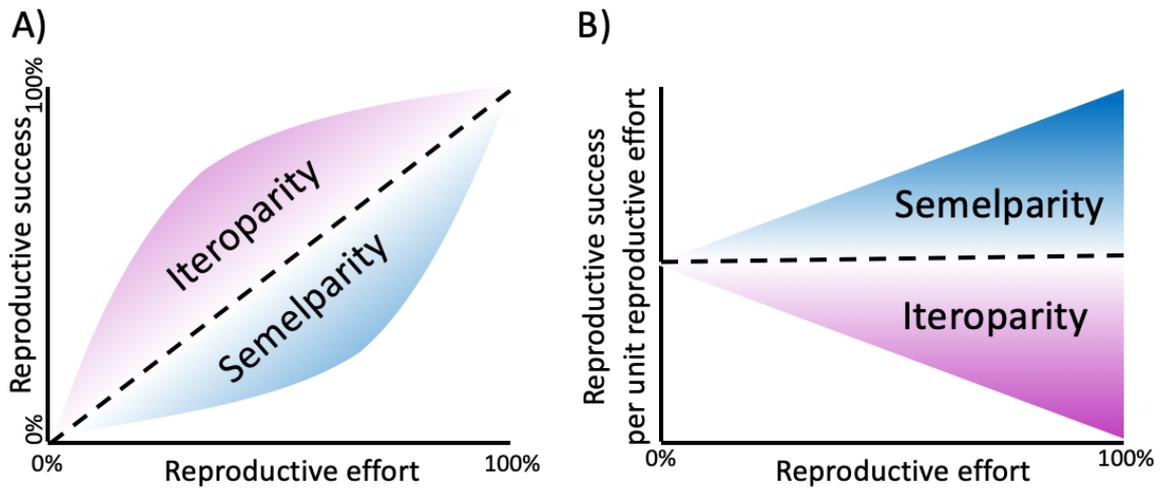


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1404 **Figure 2**

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1408 Supporting information (Appendix 1: Tables S1-10)

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1410 **Table S1.** Female invertebrates with facultative semelparity- often semelparous but can

1411 ovulate twice and raise two broods.

1412

Organism	Why lethal reproductive effort may confer greater fitness than less effort combined with iteroparity?	Proximate cause of death - reproductive effort mechanism that kills individuals	Explanation	Ref
<i>Misumena vatia</i> Goldenrod crab spider Family Thomisidae	Constraints of food availability in the short breeding season, adults unlikely to survive to next season that provides food adequate for breeding (Maine, USA).	Maternal investment of most body tissue in eggs. Starvation while guarding clutch from parasites & predators.	Females are ambush predators on a flower. Lose about two-thirds of body mass during guarding eggs and young, heavier mothers (in prey-rich sites) are fitter. Can produce smaller second clutch if supplementary fed and a warm summer, using food eaten after first brood. Female-biased adult sex ratio	(Morse 1994, Morse and Stephens 1996, LeGrand and Morse 2000, Morse 2012)
<i>Stegodyphus dumicola</i> African social spider Family Eresidae	?	Maternal investment of all body tissue (95% of mass, all but exoskeleton) via matriphagy	A social desert spider. Mothers and sometimes related virgin female helpers regurgitate body fluid for young then are eaten by young. Mothers do not eat while feeding young and guarding clutch from parasitoids & predators in nest. Investment in eggs (~90) is < 3% of maternal mass, can lay a second clutch if first is lost. Young fed more via matriphagy have higher mass at dispersal, and higher survival. In experimentally reduced broods, female mass loss per day was low and matriphagy occurred very late or not at all.	(Salomon et al. 2005, Junghanns et al. 2017)
<i>Stegodyphus lineatus</i> spider from Semi-arid Mediterranean, Israel, Asia minor. Family Eresidae	Much higher adult female mortality than juvenile mortality, due to exposure to predators and parasitoids	Maternal investment of most or all maternal body tissue via matriphagy, investment in guarding exposing female to predation	Female guarding in enclosed sheet web tube followed by matriphagy. Midgut tissue liquifies, mothers feed young with regurgitated tissue, then young pierce female's abdomen and consume her if mother is present- wasps, spiders and ants killed most females during guarding. Ovaries are the last organs to dissolve and experimental females protected from predation and matriphagy laid	(Schneider and Lubin 1997, Salomon et al. 2015)

			again and raised a second clutch, first clutch had worse growth and survival. Models showed that slightly higher adult survival favours iteroparity.	
<i>Geolycosa domifex</i> Canadian grassland burrowing wolf spider Family Lycosidae	Higher adult female than juvenile mortality due to exposure to parasitoids	Adult death is due to parasitoid wasp attack, which is triggered by maternal care behaviour	Females produce 1 clutch at 3 years old. Unseal burrows when young hatch to allow foraging, open burrows give access to pompilid wasps and >99% of adult females killed. Surviving females can breed again next season. Pre-reproductive females open burrows later, less. Juvenile mortality in 1st season ~85%	(McQueen 1978)
<i>Chiracanthium japonicum</i> Japanese sac spider Family Cheiracanthiidae	Constraints of food availability in the short breeding season, adults unlikely to survive to next season that provides food adequate for breeding, offspring become independent soon before winter (northern. Japan).	Maternal investment of all maternal body tissue via matrophagy	After mating females forage for 2 weeks then lay eggs and guard young in an enclosed nest that they construct in grassland. Maternal defence decreases predation on clutch, but mother cannot hunt or provision young other than via matrophagy. Mother removal showed that offspring survival was higher when matrophagy occurred because young can disperse at a more advanced stage with longer legs. Females are capable of further ovulation.	(Toyama 1999, Hironaka and Abe 2012)
<i>Parastrachia japonensis</i> Insect Bug in Family Pentatomidae	Constraints of food availability in the erratic breeding period, adults unlikely to survive to next time that provides food adequate for breeding	Usually starvation during provisioning and guarding young, investment via trophic eggs, sometimes matrophagy	Specialises on an erratically fruiting plant to provision young in burrows. Mother searches for fallen fruits and carries them to burrows, holds fruit to guard against kleptoparasites. Also provisions with unfertilised eggs. Young sometimes attack mother while she is holding fruit. Food available briefly, separated by long unfavorable intervals.	(Tachikawa 1985, Hironaka et al. 2007, Trumbo 2013)
<i>Paratemnodes nidificator</i> South American savanna Pseudoscorpion	Constraints of food availability in dry years, adults unlikely to survive to next post-drought time that provides food adequate for breeding	Maternal investment of all maternal body tissue via matrophagy	Matrophagy occurs in droughts. Suggested to be a response to food scarcity in poor seasons. When food is scarce, mother left the nest to trigger offspring attack. Also suggested that matrophagy reduces cannibalism in offspring.	(Tizo-Pedroso and Del-Claro 2005)

1414 **Table S2.** Female invertebrates with obligate semelparity- either cannot ovulate twice, or  
 1415 second ovulation is not viable and cannot raise a second brood.

1416

Organism	Driver- why lethal reproductive effort may confer greater fitness than iteroparity	Proximate cause of death - reproductive effort mechanism that kills individuals	Mechanism of pre-death loss of future reproductive capacity	Explanation	Reference
<i>Amaurobius ferox</i> . Black lace-weaver. Spider, Family Araneidae	?	Maternal investment of all maternal body tissue and the second (insurance) clutch via matriphagy	Reserve clutch destroyed by first brood, ovaries non-functional after two clutches, so can lay a replacement clutch but can only raise one brood.	Females have a reserve clutch in case first lost. If first brood survives, reserve clutch eaten by first brood, mother eaten by brood. Mothers consumed by first brood have higher reproductive success than if they produce a second clutch. Females can live 2 years. In captivity semelparity produced 82 healthy spiderlings per female and iteroparity (mother removed from first clutch to lay again) produced 75 under-developed spiderlings per female	(Kim et al. 2000)
<i>Lysiteles coronatus</i> Japanese crab spider Family Thomisidae	Constraints of food availability in the short breeding season, adults unlikely to survive to next season that provides food adequate for breeding (northern Japan).	Maternal investment of most body tissue in eggs. Starvation while guarding clutch from parasites & predators.	Ovaries cannot develop after guarding, so can lay a replacement clutch but can only raise one brood.	Females guard their eggs and young without eating, lose about a third of body mass during guarding eggs and young then die after raising one clutch. Some females that lose the clutch early in the season feed again and can lay a second (smaller) one.	(Futami and Akimoto 2005)
<i>Australomisdia</i> (Dicaea) <i>ergandros</i> Australian crab Spider (Eucalypt forest) Family Thomisidae	?	Maternal investment of all maternal body tissue and degraded trophic egg clutch (too large to lay) via matriphagy	Ovaries degrade after the female lays one clutch.	Young feed on degraded trophic eggs imbibed through leg joints, then the mother's tissue. Suggested that decreasing sibling cannibalism is a fitness benefit that	(Evans 1998)

				could compensate for loss of iteroparity.	
<i>Stegodyphus sarasinorus</i> spider Family Eresidae	?	Maternal investment of all maternal body tissue via matrophagy	Gut and organs dissolve during regurgitation feeding and cannot recover	Mother guards eggs and spiderlings on a sheet web and doesn't feed during guarding. Mother feeds young regurgitated tissue then her whole body. Young disperse after the mother is reduced to only exoskeleton over three weeks.	(Deshmukh 2015)
<i>Stegodyphus pacificus</i> spider Family Eresidae	?	Maternal investment of all maternal body tissue via matrophagy	Gut and organs dissolve during regurgitation feeding and cannot recover	Mother makes a web sheet cocoon with prey stores inside to maintain her during guarding, seals entrance, feeds young with regurgitated tissue then her whole body. Young disperse about three months after eggs laid, when maternal tissues depleted.	(Tripathi et al. 2020)
<i>Anechura harmandi</i> Japanese hump earwig Insect order Dermaptera, Family Forficulidae (and at least 3 European species in this Family)	High predation on adults. Possible constraints of food availability in short breeding season, adults unlikely to survive to next season that provides food adequate for breeding (low latitude subalpine regions)	Maternal investment of all maternal body tissue via matrophagy	Ovaries degrade after the female lays one clutch and cannot develop again.	Dermapterans have eggs that need maternal care to hatch. Evolution of matrophagy associated with colonisation of subalpine environments (3 phylogenetic origins in Europe). Matrophagy increases offspring survival in cold areas where food is scarce-removing mother and offering food to nymphs increases survival similarly. However predation not starvation causes high mortality of adult <i>A. harmandi</i> .	(Kohno 1997, Guillet and Vancassel 2001, Suzuki et al. 2005)
<i>Graneledone boreopacifica</i> Cephalopod Mollusc, Family Megaleledonidae (and other Octopus, Family Octopodidae, other	Suggested high adult mortality due to predation by fish on soft-bodied cephalopods (however contrasting pelagic juvenile survival not quantified)	Starvation during guarding eggs and young	Octopus cannot ovulate twice or raise a second brood. Optic gland is part of the mechanism as secretions halt feeding	In <i>G. boreopacifica</i> , brooding, guarding, and gradual exhaustion of body reserves over 53 months. Brooding female does not feed and will not accept offered food. Soft eggs of octopus would be vulnerable to predators if not guarded. Female	(Wodinsky 1977, Aronson 1991, Rocha et al. 2001, Robison et al. 2014, Wang and

cephalopods in Subclass Coleoidea, ~930 spp)				semelparity is ancestral in octopus. Some taxa can split their one batch of gametes into broods / spawning events. Hormones secreted by optic gland (catecholamine, steroid, insulin, feeding peptides) regulate feeding, brooding and tissue loss in <i>O. bimaculoides</i> . Gland removal causes feeding resumption and prolongs life (by months), but does not cause gonad recovery.	Ragsdale 2018)
<i>Caenorhabditis elegans</i> Nematode	?	Maternal investment in yolk (which is expelled and has a function similar to lactation) depletes gut, fat & liver tissue	Yolk manufacture triggered by maturity causes irreversible tissue atrophy and individual cannot breed again	Hermaphrodites make and store sperm in their male function, ovulate and lay eggs in their female function, then make and release yolk outside the body to feed offspring. Preventing sexual maturity prevents gut conversion to yolk and extends lifespan	(Kern and Gems 2022)
<i>Paracerceis sculpta</i> Marine isopod in the family sphaeromati dae	Suggested higher adult than juvenile mortality, due to risky breeding migration in adults. Juveniles are initially protected inside sponges (however they must also migrate to feeding habitat)	Maternal investment of most maternal body tissue via transfer during incubation inside body cavity. Tissue depletion	Mouthparts become fused to the head so females cannot feed after maturity. Irreversible tissue atrophy and individual cannot breed again	Females brood young in the body cavity, don't eat while brooding. Young absorb nutrients from body fluid, deplete lipids, hepatopancreatic tissue and muscle. High risk of adult death while migrating between feeding (offshore algal beds) and breeding habitat (intertidal sponges). Juveniles are carnivorous.	(Shuster 1991)

1418 **Table S3.** Female vertebrates with facultative semelparity- semelparous but have no pre-  
 1419 breeding mechanism that destroys future ovulation capacity (no loss of gonad function  
 1420 distinct from programmed death).

1421

<b>Organism</b>	<b>Driver- why lethal reproductive effort may confer greater fitness than iteroparity</b>	<b>Proximate cause of death - reproductive effort mechanism that kills individuals</b>	<b>Explanation</b>	<b>Ref</b>
Pacific salmon <i>Oncorhynchus</i> ( <i>O. tshawytscha</i> , <i>kisutch</i> , <i>nerka</i> , <i>keta</i> , <i>gorbuscha</i> ) chinook, coho, sockeye, chum, and pink salmon Fish Family Salmonidae	Much higher adult mortality than juvenile mortality, due to risky and energy-intensive upstream breeding migration in adults	Females deplete energy stores investing in large eggs and competition over spawning sites. Programmed depletion mechanism of reproductive death. Loss of corticosteroid binding capacity, so escalating circulating stress hormones, reducing immune function & causing tissue disintegration	Semelparity evolved in the late Miocene 5-10 mya, when low sea levels exacerbated risky breeding migration from the sea. Clade evolved large eggs.	(Unwin et al. 1999, Barry et al. 2001, Crespi and Teo 2002, Crespi 2004, Hruska et al. 2010, Macquoen and Johnston 2014, Kindsvater et al. 2016)
<i>Mallotus villosus</i> Capelin Fish Family Osmeridae	Suggested higher adult than juvenile mortality in semelparous populations due to intensive offshore fishing	Females presumably deplete energy stores investing in large eggs	Data are from fishing samples. Deep water ocean-spawning populations are semelparous in both sexes, have larger eggs than beach-spawning iteroparous populations	(Huse 1998, Christensen et al. 2008)
<i>Plecoglossus altivelis</i> Ayu Fish Family Osmeridae	Suggested that fish that can invest in growth (perhaps in productive territories with more algae cover) exposed to size-selective predatory birds	Large females invested more energy in eggs soon before spawning, depleting energy, fat and protein	Algae-eating river fish with a single breeding season. Females with productive territories grow much faster. Large females are semelparous, gonads can be 30% of body mass. Small females in the same population spawn twice two weeks apart. No genetic basis of two strategies	(Iguchi and Tsukamoto 2001)
<i>Oncorhynchus mykiss</i> Steelhead trout / rainbow trout Fish Family Salmonidae	Higher adult mortality than juvenile mortality where streams are longer, due to risky energy-intensive upstream breeding migration in adults	Females presumably deplete energy stores investing in eggs and competition over spawning sites	Trout migrate from the ocean to rivers at maturity. More trout are semelparous at sites where upstream migrations are longer	(Finch and Rose 1995)

<p><i>Neotoma lepida</i> Desert woodrat Mammal Family Cricetidae</p>	<p>Much higher adult mortality than juvenile mortality in hot locations (Death Valley USA) and years, due to overheating of large individuals</p>	<p>Females expose themselves to overheating when they invest in high fecundity (body size-litter size correlation).</p> <p>Overheating</p>	<p>Typically iteroparous, but one desert population is semelparous in hot years because the large body size that maximises fecundity is lethal in summer, persistence at a smaller size would not compensate. Survival over summer thus trades off with reproductive effort only in very hot years and locations</p>	<p>(Smith and Charnov 2001)</p>
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1423 **Table S4.** Female vertebrates with obligate semelparity- cannot ovulate more than once.

1424

<b>Organism</b>	<b>Driver- why lethal reproductive effort may confer greater fitness than iteroparity</b>	<b>Proximate cause of death - reproductive effort mechanism that kills individuals</b>	<b>Mechanism of pre-death loss of future reproductive capacity</b>	<b>Explanation</b>	<b>Ref</b>
<i>Conger conger</i> European conger eel Fish Family Congridae	Much higher adult mortality than juvenile mortality, due to energy-intensive breeding migration to specific area of abyssal ocean depth in adults	Maternal investment of most body tissue in in large number of eggs. Skeleton and jaws atrophy, teeth fall out, buoyancy fails, tissue depletion leads to inability to surface or feed. Programmed reproductive death.	Ovary development can only occur once as it fills body cavity and consumes all body fat and most calcium from the skeleton.	Females live in different habitat (100-400m ocean depth) to males (600-800m depth). Females can live >20 years. Ovaries mature synchronously during migration to species-specific deep ocean (3 km) spawning grounds, before mating. Clade evolved in deep ocean.	(Bell 1980, Casadevall et al. 2017)
<i>Conger orbignianus</i> Southern conger eel Fish Family Congridae	Energy-intensive breeding migration to specific area of abyssal ocean depth in adults	Maternal investment of most body tissue in large number of eggs. Skeleton and jaws atrophy, teeth fall out, buoyancy fails, tissue depletion leads to inability to surface or feed, and programmed reproductive death. Death occurs in aquaria- mechanism is not migration effort	Ovary development can only occur once as it fills body cavity and consumes all body fat and most calcium from the skeleton.	Females live in shallow ocean for several years until their spawning migration to deep ocean. In captivity females switch their behaviour suddenly to cease feeding, abdominal cavity becomes completely filled by hypertrophied ovaries, and they move to shelters in the aquarium where they die.	(Bell 1980, Figueroa et al. 2009)
<i>Anguilla japonica</i> and other <i>Anguilla</i> species Eels in the Fish Family Anguillidae	Much higher adult mortality than juvenile mortality during energy-intensive breeding migration in the open ocean to specific subtropical spawning areas (which can be large, e.g. 2000 km across), Breeding	Maternal investment of much body tissue in large number of eggs (many millions, >100m in one species). Mass of a wild female at beginning of spawning was ~50% gonads /eggs. Programmed	Can only ovulate once- ovary development causes irreversible tissue loss	Eels are adaptable, physiologically resilient benthic carnivores. Females can live in freshwater habitat for 25-60 years before maturity and ocean migration. Adults leaving fresh water do not yet have	(Tsukamoto et al. 2011, Jellyman 2021)

	migration is often thousands of kilometres, partly against the prevailing current, takes ~ 6 months to reach spawning grounds.	reproductive death. Spawning adult <i>A. japonica</i> caught in the wild had tooth loss due to decalcification, atrophied digestive tracts, and were depleted except for gonads, fins, and enlarged eyes.		developed gonads. Larvae are transported back to parent's area of origin on prevailing currents, but most perish in unfavourable currents. Possibly splits clutch over spawning events 2-3 months ( <i>A. japonica</i> spawns at new moon).	
<i>Lampetra fluviatilis</i> River lamprey Agnathan fish Family Petromyzontidae	Higher adult mortality than juvenile mortality, due to energy-intensive breeding migration upstream	Depletion of most body tissue, programmed reproductive death. Material for egg development mainly from fat and protein of body wall- skin, muscle, and connective tissue. Post-spawning wild lampreys often covered by fungus. If infection, migration, nesting, mating prevented, all still die soon after ovulation in captivity.	Ovary development causes irreversible tissue loss, gut atrophy and can only occur once	Adults migrate from the sea into a river at maturity to spawn. Tissue disintegration follows ovulation, and there is a loss of circadian cycle at spawning.	(Bell 1980, Larsen and Dufour 1993)

1426 **Table S5.** Plants with facultative semelparity- often semelparous but can survive flowering

1427 and can be triggered to flower repeatedly.

1428

<b>Organism</b>	<b>Driver- why lethal reproductive effort may confer greater fitness than iteroparity</b>	<b>Proximate cause of death - reproductive effort mechanism that kills individuals</b>	<b>Explanation</b>	<b>Ref</b>
Bamboo. Many woody subtropical & temperate species, plant subfamily Bambusoideae, Family Poaceae	Parent death creates widespread fuel load that collects lightning strikes and causes fire that enables seedling recruitment at the fire scale. Seeds drop under parent and flowering is synchronised at this scale.	Investment of nutrients and tissue in high seed production at expense of survival. Tissue depletion including the rhizome.	Densely packed clonal clumps with vigorous rhizomes grow for 20-100 yrs, eventually inhibit growth and reproduction. Seeds drop at base of spent parent. Some species of bamboo can reportedly survive flowering if heavily fertilised and protected from competition.	(Janzen 1976, Keeley and Bond 1999)
<i>Beta patula</i> Wild beet plant Family Amaranthaceae	Low nutrients constrain plant to invest in reproduction at expense of survival rather than to distribute limited effort across additional rosettes	Investment of nutrients and tissue in flowering / high seed production at expense of survival Tissue depletion.	Wild beet can become iteroparous by producing more rosettes if nutrients are decreased, semelparity is associated with ability to invest in reproduction under high nutrient conditions	(Hautekeete et al. 2001)
<i>Oenothera</i> species Evening primrose, Plants, Family Onagraceae	Higher adult mortality and lower juvenile mortality in locations and times with hot dry seasons, due to physiological stress affecting large individuals, and reduced shading of seedlings. Plants expose themselves to overheating and drought stress if they invest in growth	Investment of nutrients and tissue in flowering / high seed production at expense of survival Tissue depletion.	Comparative analysis of species shows that aridity with heat is associated with semelparity. Drought alone can favour dormancy rather than semelparity.	(Evans et al. 2005)
<i>Ipomopsis aggregata</i> Scarlett gilia Plant Family Polemoniaceae	High pollinator availability allows plant to invest in reproduction at expense of survival. <i>why does this benefit them ?</i> Low pollinator availability triggers plant to distribute effort across additional rosettes.	Investment of nutrients and tissue in flowering / high seed production at expense of survival Tissue depletion.	Can become iteroparous by producing an ancillary rosette if pollinators are excluded or flowers removed, reducing fruit set below 40%	(Paige and Whitham 1987)
<i>Lobelia telekii</i> Mount Kenya rosette plant. Plant Family Campanulaceae	Higher adult mortality and lower juvenile mortality in dry locations	Investment of nutrients and tissue in flowering / high seed production at expense of survival Tissue depletion.	In drier sites, lobelias flower infrequently, have high mortality between reproductive episodes - low chance of future reproduction compensated by high	(Young 1990)

			fecundity at expense of adult survival.	
<i>Erysimum capitatum</i> Western wallflower Plant Family Polemoniaceae	Plants that invest in growth of additional rosettes thus distribute reproductive effort expose themselves to drought stress, which is more likely to kill them before reproduction than if they limit water loss by restricting themselves to one flowering rosette.	Investment of nutrients and tissue in flowering / high seed production at expense of survival - Tissues of the single reproductive rosette disintegrates during flowering / seed production. Tissue depletion.	Semelparous individuals occur at low elevation where water is scarce in summer, produce fewer rosettes as juveniles, reducing water loss. Semelparous plants flower from a single apical rosette.	(Kim and Donohue 2012)
<i>Cynoglossum officinale</i> Houndstongue Plant Family Boraginaceae	Higher adult mortality and lower juvenile mortality caused by size-specific predation.	Investment of nutrients and tissue in flowering / high seed production at expense of survival Tissue depletion.	A weevil preferentially attacks and kills large individuals. Evidence that natural enemies are responsible, as it is semelparous in native range and in the parts of introduced range where weevil is introduced for biocontrol.	(Duncan and Williams 2020)
<i>Bellis annua</i> , <i>Bellis microcephala</i> Plant Family Asteraceae	Higher adult mortality in locations with summer drought.	Presumably investment of nutrients and tissue in flowering / high seed production at expense of survival Tissue depletion.	Phylogeny reconstruction shows that annuals evolved three times independently, corresponding to evolutionary transitions from cool, wet environments to Mediterranean locations with summer drought.	(Fitz et al. 2002)
<i>Heliophila spp</i> Plant Family Brassicaceae	Higher adult mortality and lower juvenile mortality in locations with frequent droughts, because annuals escape drought-prone seasons as resilient seeds.	Presumably investment of nutrients and tissue in flowering / high seed production at expense of survival Tissue depletion.	Comparative analysis of species shows that locations of frequent drought co-occur with evolutionary transitions to semelparity (annuals).	(Monroe et al. 2019)

1430 **Table S6.** Plants with obligate semelparity- cannot survive reproduction.

1431

<b>Organism</b>	<b>Driver- why lethal reproductive effort may confer greater fitness than iteroparity</b>	<b>Proximate cause of death - reproductive effort mechanism that kills individuals</b>	<b>Explanation</b>	<b>Ref</b>
<i>Agave deserti</i> Desert agave, Plant Family Asparagaceae	High reproductive effort may provide disproportionately high fitness benefits, so no extrinsic adult-biased mortality explanation needed	Investment of nutrients and tissue in flowering / high seed production at expense of survival -investment in large flower stalk exceeds photosynthesis and water transport capability, so plant dies. Tissue depletion (autophagy).	Suggestion that pollinators prefer taller inflorescences and proportional fruit set increases with inflorescence height. However some experimental evidence fails to support this mechanism (Young 1991)	(Nobel 1977, Schaffer and Schaffer 1979, Young and Augspurger 1991)

1432

1433 **Table S7.** Male invertebrates with facultative semelparity- often semelparous but capable of  
 1434 further spermatogenesis.

1435

<b>Organism</b>	<b>Driver- why lethal reproductive effort may confer greater fitness than iteroparity</b>	<b>Proximate cause of death - reproductive effort mechanism that kills individuals</b>	<b>Explanation</b>	<b>Ref</b>
<i>Tenodera sinensis</i> Chinese mantid Insect	Higher adult mortality- extrinsic (misadventure, predation, starvation)	Paternal investment of all paternal body tissue via sexual cannibalism	Sexual cannibalism. Female uses male body and materials in the ejaculate as nutrition for offspring production. Male body tissue can be most of the diet of adult females, food limited. Males should avoid being cannibalised at $\geq 20\%$ chance of remating.	(Hurd 1989, Brown and Barry 2016)
<i>Argiope keyserlingi</i> St Andrew's cross spider, Family Araneidae	? Higher adult mortality- extrinsic (misadventure, predation, starvation)	Paternal investment of all paternal body tissue via sexual cannibalism	Males can only use a pedipalp once, sperm on pedipalps is not replenished. Insert one or two pedipalps, older males cease sperm production. Sexual cannibalism on 1st or 2nd copulation, does not change fecundity. Sometimes 2nd mating is a different virgin female. Little or no mate guarding.	(Herberstein et al. 2005, Michalik and Rittschof 2011)
<i>Pogonomyrmex barbatus</i> (and <i>P. rugosus</i> , <i>P. desertorum</i> , <i>P. maricopa</i> ) Harvester ants. Hymenopteran insect Family Formicidae	Female synchrony and lek-like aggregation escalating competition between males	Some males die during mating- females bite abdomen of copulating males after several minutes, severing male genitals. Lethal tissue investment in mate-guarding.	Two to ten males compete vigorously to grip female and remain attached in a mating aggregation. Males can survive and join further aggregations. Females seen with bitten-off aedeagus attached. Apparently females can't remove males intact to gain more mates, males benefit by forcing dismemberment to form a plug.	(Holldobler 1976)

1436

1437 **Table S8.** Male invertebrates with obligate semelparity- incapable of further spermatogenesis

1438 and or copulation.

1439

<b>Organism</b>	<b>Driver- why lethal reproductive effort may confer greater fitness than iteroparity</b>	<b>Proximate cause of death - reproductive effort mechanism that kills individuals</b>	<b>Mechanism of pre-death loss of future reproductive capacity</b>	<b>Explanation</b>	<b>Ref</b>
<i>Latrodectus hasselti</i> Redback spider Family Theridiidae	Suggested higher adult male than juvenile male mortality due to misadventure, predation, and starvation during mate searching (however there is lethal competition for paternity success, suggesting that multiple males find females)	Sexual cannibalism associated with paternity success. Males often trigger sexual cannibalism by flipping into the female's mouth during copulation.	Many males insert both palps in the one female, and ends break off during copulation making them sterile.	Sexual cannibalism increases paternity success by reducing female re-mating. Second mate search is rarely successful before male dies- males are small and females spatially dispersed.	(Forster 1992, Andrade 1996, Andrade 2003)
<i>Dolomedes tenebrosus</i> Dark fishing spider. Family Pisauridae	Rapid male maturity at small size, male-biased sex ratio (3:1), intense post-mating competition between males	Males die spontaneously during sperm transfer, as a result of haematodochal bulb (end of palp) inflating to plug female opening as a form of mate-guarding, draining body fluid from the male. Lethal tissue investment in mate-guarding.	Haematodochal bulb is fixed in inflated state once expanded and cannot be used again	Obligate male death facilitates sexual cannibalism. Pedipalp remains in female with attached dead male (but does not prevent polyandry). 100% post-mating sexual cannibalism. Both pedipalps are viable. Males are not limited by their ability to encounter additional females	(Schwartz et al. 2014, 2016)
<i>Tidarren sisyphoides</i> North American comb-footed spider, Family Theridiidae	Rapid male maturity at small size, male-biased sex ratio, shortage of receptive females, intense searching and pre-mating competition between males	Males die spontaneously during copulation. Palp insertion and inflation causes male shrivelling and death during or soon after mating. Lethal tissue investment in mate-guarding.	Just before sexual maturity, male amputates one pedipalp (10% of body mass). Haematodochal bulb is fixed in inflated state once expanded and cannot be used again	Males can insert one pedipalp only once. Speed and endurance increased after pedipalp removed- both aerobic and anaerobic movement. Emasculation improves endurance during competitive searching and mobility in contest on the female's web. Up to 25 males found on a female's web just before female maturity.	(Knoflach and Benjamin 2003, Ramos et al. 2004)

				No sexual cannibalism.	
<i>Tidarren argo</i> North African comb-footed spider, Family Theridiidae	Likely rapid male maturity at small size, male-biased sex ratio, shortage of receptive females, intense competition between males	Sexual cannibalism. Males always eaten by female during copulation	At penultimate moult just before sexual maturity, male amputates one pedipalp. Males can insert one pedipalp in female, once only. Haematodochal bulb is fixed in inflated state once expanded and cannot be used again.	Female amputates the other pedipalp on insertion. Haematodochal bulb has a holdfast structure, continues to plug female opening and deliver sperm for 4 hours. Suggested that emasculation accelerates male maturity giving males more time to find a female.	(Knoflach and van Harten 2001)
<i>Tidarren cuneolatum</i> North African comb-footed spider, Family Theridiidae	Rapid male maturity at small size, male-biased sex ratio, shortage of receptive females, intense competition between males	Palp insertion and inflation causes male shrivelling and death during or soon after mating. Female often eats male. Lethal tissue investment in mate-guarding, and sexual cannibalism.	At penultimate moult just before sexual maturity, male amputates one pedipalp and eats contents. Haematodochal bulb is fixed in inflated state once expanded and cannot be used again	Males mature and mate 1.5 months old, live on female web before mating. Multiple males on a web do not fight but court competitively. Pedipalp is not large in relation to body size, and size dimorphism and development time not unusual for the clade.	(Knoflach and Van Harten 2000, 2001)
<i>Argiope aurantia</i> yellow garden spider, Family Araneidae	Intense post-mating competition between males	All males die spontaneously on insertion & inflation of haematodochal bulb of second pedipalp, before females bite them. Lethal tissue investment in mate-guarding.	Haematodochal bulb is fixed in inflated state once expanded and cannot be used again	Males attempt to inseminate both female openings, first palp insertion is brief, males jump off, court again and insert second palp. Males compete and attempt to dislodge unresponsive / dead males anchored by inserted palp (usually unsuccessfully). Because the palps of dead males are fixed in the inflated state so are harder to remove than live males, dead males act as whole-body mating plugs, often preventing other males mating.	(Foellmer and Fairbairn 2003)
<i>Argiope aemula ovalis</i> St Andrew's	Likely post-mating competition between males	Males die spontaneously during mating. On insertion of	Likely that haematodochal bulb is fixed in inflated	Males attempt to inseminate both female openings, first palp insertion is brief,	(Sasaki and Iwahashi 1995)

cross spider, Family Araneidae		second palp, all males that are not pulled out of the female (with tweezers) before 60 seconds elapsed died. One died without being cannibalised, others eaten by female when unresponsive. Lethal tissue investment in mate-guarding. and Sexual cannibalism.	state once expanded and cannot be used again, as in <i>A. aurantia</i>	males jump off, court same female gain and insert second palp.	
<i>Nephila clavipes</i> Golden orb-web spider Family Nephilidae	Females are much larger than males. Males rarely feed as adults as they leave their webs, so they are vulnerable to starvation. Intense post-mating competition between males.	Starvation during mate-guarding while male remains on female's web.	Testes cease producing sperm before maturity, all sperm transferred to the pedipalps.	Males inhabit female web before and after mating, often use both palps for same female, can mate-guard after mating for more than 2 weeks. Suggested males improve endurance for mate-guarding by diverting energy from testes to muscles. No emasculation, little sexual cannibalism. Females are promiscuous and are receptive while feeding, males often mate rather than feed on the female's prey item. Males live ~2 months after reaching female's web.	(Christensen et al. 1985, Cohn and Christensen 1987, 1988, Michalik and Rittschof 2011)
<i>Nephilengys malabarensis</i> Hermit spider, Family Araneidae	Intense post-mating competition between males	Paternal investment of all paternal body tissue via sexual cannibalism. Energy depletion and tissue investment in fighting & mate-guarding.	All males break off one or both palps during mating, making them sterile.	75% are eaten by female during mating, the remaining 25% mate-guard and have improved fighting ability against intact males after palps (9% of body mass) removed, proportionate to mass loss. Emasculation improves endurance. Large palps may improve mating success so they don't sever them until mating.	(Lee et al. 2012)

<i>Nephilengys borbonica</i> La Reunion & Mayotte Islands hermit spider, Family Araneidae	Intense post-mating competition between males	Energy depletion and tissue investment in fighting & mate-guarding. Sometimes paternal investment of all body tissue via sexual cannibalism	Suggested males always break off palps to plug female opening, making them sterile.	Female partially or completely remove mating plugs. Whole and partial plugs can inhibit successful mating by subsequent males, aggressive mate-guarding observed. Some sexual cannibalism	(Kuntner et al. 2009)
<i>Apis mellifera</i> European honey bee Hymenopteran insect Family Apidae	Male-biased sex ratio, escalating competition between males because there are many drones and one receptive queen. Queen probably benefits from post-copulatory sperm selection / sperm competition	Endophallus is torn off during brief copulation in flight, killing the male and leaving a plug structure behind ('mating sign'). Lethal tissue investment in mate-guarding.	In honey bees (and other social insect males) spermatogenesis ceases during the pupal stage. Endophallus eversion is irreversible.	In honey bees the queen mates with many drones. Intense sperm competition / cryptic female choice is likely- volume in bursa is much greater than oviduct and only ~2.5% are stored by the queen contracting the bursa to transfer sperm into oviducts.	(Baer 2005)
<i>Dinoponera quadricaps</i> Brazilian queenless ponerine ant. Hymenopteran insect Family Formicidae	Males outnumber sexually receptive workers, and a male has little chance of finding a second nest where he could mate again	During mating the female severs the end of male's abdomen, male genitalia remain attached to her genital tract. Lethal tissue investment in mate-guarding.	Spermatogenesis ceases during the pupal stage. Loss of male genitalia during mating	Mating is synchronised outside a nest before dispersal. Female removes severed male genitalia after ~30 minutes. Mating plug prevented immediate re-mating, females apparently do not re-mate later.	(Monnin 1998)

1441 **Table S9.** Male vertebrates with facultative semelparity- often semelparous but capable of

1442 further spermatogenesis

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<b>Organism</b>	<b>Driver- why lethal reproductive effort may confer greater fitness than iteroparity</b>	<b>Proximate cause of death - reproductive effort mechanism that kills individuals</b>	<b>Explanation</b>	<b>Ref</b>
<i>Urocitellus parryii</i> Arctic ground squirrel Mammal Family Scuridae	Female synchrony escalating competition between males. Females are synchronised because of short arctic breeding season	Male fighting, mass loss, injuries	80% of breeding male arctic ground squirrels die each year, 50% during the ~3 week mating season, others during hibernation. Sexual selection associated with stress hormone rise.	(Boonstra et al. 2007, Edwards et al. 2016)
<i>Parantechinus apicalis</i> and <i>Dasyurus hallucatus</i> . Dibbler and northern quoll. Mammal Family Dasyuridae	Female reproductive synchrony with season of peak food escalating competition between males	Male competition, exhaustion, stress. Lethal tissue investment in mate-guarding.	Seasonally predictable annual spike in food abundance selects for short mating period and monoestry, females drive male sperm competition and intense mate-guarding by restricting receptivity period and engaging in polyandry. Semelparity less frequent where relative size of the food peak is relaxed (dibblers on an island with ultra fertile soil), or when male competition is relaxed by lower population density (mainland sites. Islands with high density show near-complete semelparity). Males show fur loss and lose weight, but can recover. Stress but no extreme circulating corticosteroids- no loss of corticosteroid binding globulin in these genera.	(Fisher et al. 2013)
<i>Furcifer labordi</i> Labord's dwarf chameleon Reptile Family Chamaeleonidae	Higher adult mortality than juvenile mortality associated with small adult size, and protected environment of juveniles. Suggested escalating competition between males is due to short wet season	Male fighting, mass loss, injuries	Most of the life cycle is an egg stage. Adult males rarely survive to breed a second time in area with short breeding (wet) season. In location and time with a long wet season, both sexes can breed a second time.	(Karsenton et al. 2008, Eckhardt et al. 2017)
Pacific salmon <i>Oncorhynchus</i> ( <i>O. tshawytscha</i> , kisutch, nerka, keta, gorbuscha)	Much higher adult mortality than juvenile mortality, due to risky and energy-intensive upstream breeding migration in adults	Spawning is associated with escalating stress hormones, reduced immune function, tissue disintegration. In sockeye salmon	Although often considered obligate semelparous, Pacific salmon have no pre-mortality mechanism precluding future breeding. ~6% of hatchery-raised male chinook salmon in NZ recovered & spawned a 2nd & 3rd time. Gonads functioned, lower gonad mass than	(Unwin et al. 1999, Barry et al. 2001, Crespi and

<p>chinook, coho, sockeye, chum, pink salmon Fish Family Salmonidae</p>		<p>free corticosteroid level increases ~60-fold in spawning males due to loss of corticosteroid binding globulin. Energy depletion and tissue investment in fighting &amp; mate-guarding</p>	<p>first spawning. Poor seawater tolerance after maturity likely precludes repeat migration in wild fish. Males deplete energy stores via reproductive competition over females and spawning sites, and have more investment in secondary sexual traits than do iteroparous relatives</p>	<p>Teo 2002, Crespi 2004, Hruska et al. 2010, Macqu een and Johnsto n 2014, Kindsv ater et al. 2016)</p>
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1445 **Table S10.** Male vertebrates with obligate semelparity- incapable of further spermatogenesis

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Organism	Driver- why lethal reproductive effort may confer greater fitness than iteroparity	Proximate cause of death - reproductive effort mechanism that kills individuals	Mechanism of pre-death loss of future reproductive capacity	Explanation	Ref
<i>Antechinus stuartii</i> (and <i>A. agilis</i> , other <i>Antechinus</i> spp) Brown antechinus (agile antechinus, others) Mammal Family Dasyuridae	Females escalate intense male competition by restricting and synchronising their receptive period to a few days once in the year, and engaging in polyandry.	Males die spontaneously at 11.5 months old. Programmed depletion mechanism - reproductive death. Rise in testosterone is associated with escalating stress hormones, tissue disintegration, internal bleeding and immune system collapse soon after mating. Lethal tissue investment in mate-guarding.	Testes mature and sperm move to the epididymis 6 weeks before death, spermatogenesis ceases irreversibly 4 weeks before mating. Males lose sperm continually in urine so are sterile by the end of the mating period. Mating is 2-3 weeks before death.	Seasonally predictable annual spike in food abundance selects for short mating period and monoestry in females, which causes intense competition among males. Copulations are typically 12-14 hours each, involving a 'mating lock' in which the base of the penis swells to anchor the male in place, and a mating plug. Prior loss of spermatogenesis suggested to maximise energy allocation to competitive searching, mating, mate guarding.	(Taggart and Templesmith 1991, Taggart et al. 1993, Fisher et al. 2006, Fisher et al. 2013)
<i>Phascogale calura</i> (and <i>P. tapoatafa</i> ) Red-tailed phascogale (brush tailed phascogale) Mammal Family Dasyuridae	Females escalate intense male competition by restricting and synchronising their receptive period once in the year, and engaging in polyandry.	Males die spontaneously at 11.5 months old. Programmed depletion mechanism - reproductive death similar to <i>Antechinus</i> spp Lethal tissue investment in mate-guarding.	As in closely-related antechinus spermatogenesis ceases irreversibly at maturity ~ a month before mating	Seasonally predictable annual spike in food abundance selects for short mating period and monoestry, females drive male competition by restricting receptivity period and engaging in polyandry.	(Fisher et al. 2013)
<i>Anguilla japonica</i> and other <i>Anguilla</i> species Eels in the Fish Family Anguillidae	Much higher adult mortality than juvenile mortality during energy-intensive breeding migration in the open ocean to specific subtropical spawning areas (which can be large, e.g. 2000 km across), Breeding migration is often thousands of kilometres, partly against the	Investment of much body tissue in spermatogenesis. Broadcast spawners with huge volume of gametes. Programmed reproductive death. Spawning adult <i>A. japonica</i> in the wild had tooth loss due to decalcification, atrophied digestive tracts, and were depleted except for gonads, fins, and enlarged eyes.	Can only spermiate once- causes irreversible tissue loss	Eels are adaptable, physiologically resilient benthic carnivores. Females can live in freshwater habitat for 25-60 years before maturity and ocean migration. Adults leaving fresh water do not yet have developed gonads. Larvae are transported back to parent's area of origin on prevailing currents, but most perish in unfavourable currents. Possibly splits sperm over spawning events 2-3 months ( <i>A. japonica</i>	(Tsukamoto et al. 2011, Jellyman 2021)

	prevailing current, takes ~ 6 months to reach spawning grounds.			spawns at new moon, once in a month).	
<i>Lampetra fluviatilis</i> River lamprey Agnathan fish Family Petromyzontidae	Higher adult mortality than juvenile mortality, due to energy-intensive breeding migration upstream	Depletion of most body tissue, programmed reproductive death. Post-spawning wild lampreys often covered by fungus. If infection, migration, nesting, mating prevented, all still die soon after spermiation in captivity.	Gonad development causes irreversible tissue loss, gut atrophy and can only occur once	Adults migrate from the sea into a river at maturity to spawn. Tissue disintegration follows gonad development, and there is a loss of circadian cycle at spawning.	(Bell 1980, Larsen and Dufo ur 1993)

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