

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

Diana O. Fisher¹ & Roberto Salguero-Gómez²

¹ School of Biological Sciences, University of Queensland, St Lucia 4072, Queensland, Australia

² Department of Biology, University of Oxford, 11a Mansfield Rd, OX1 3SZ, Oxford, United Kingdom

¹ Corresponding author (and contact author) d.fisher@uq.edu.au

Key words/phrases

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

Abstract

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

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

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

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

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

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

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

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

The two main classes of driver models

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

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

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

Mechanisms of death in semelparous organisms

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

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

Mechanisms of sterility in obligate semelparous organisms

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

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

Pathways to semelparity

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

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

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

Pathways to obligate semelparity in females

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

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

Some authors suggest that extreme maternal care, such as matrophagy and starvation while brooding evolved because high maternal investment is necessary for offspring survival (e.g. in the Japanese sac spider, *Chiracanthium japonicum*, Appendix 1: Table S1). However, this 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, mast seeding 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

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

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

Pathways to obligate semelparity in males

Male pre-copulatory competition and the demographic model

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

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

Male post-copulatory competition and the reproductive effort model

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

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

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

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

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

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

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

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

Why are there are no semelparous males in plants?

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

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

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

Semelparity in small mammals

Dasyurid marsupials in the genera *Antechinus*, *Phascogale*, and *Dasykaluta* are often considered to be the only semelparous terrestrial vertebrates (e.g. Kern and Gems 2022). However, there are several published investigations of semelparity in other small mammals including both male and female rodents and didelphid marsupials. Female examples include the Death Valley population of the desert woodrat *Neotoma lepida*, which is semelparous in hot years because the large body size that maximises fecundity is lethal in summer, and persistence at a smaller size would not achieve the same lifetime reproductive output over two seasons (Smith and Charnov 2001). Male examples include Arctic ground squirrels *Urocyon parryi*. 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 *Ningaui 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

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

Trade-offs and plasticity in semelparous organisms

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

Energy constraints and trophic level

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

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

Extreme environments such as hot, dry deserts or high-latitude cold ocean depths constrain 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

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

Data gaps and modelling opportunities

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

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

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

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

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

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

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

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

Why is obligate semelparity rare?

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

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

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

Conclusions

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

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

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

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

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

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

Acknowledgments

We thank S.P. Blomberg for comments and Niv DeMalach for access to preprint data. D.O.F. was supported by a UQ Principal Research Fellowship. R.S-G. was supported by a NERC Independent Research Fellowship (NE/M018458/1).

Author Contributions

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

Conflict of Interest Statement

We declare no conflicts of interest.

References

- Acker, P., R. Alexandre, R. Bourget, and B. Colas. 2014. Heterogeneity of reproductive age increases the viability of semelparous populations. *Functional Ecology* 28:458-468.
- Allen, W. 2003. Plant blindness. *Bioscience* 53:926-926.
- Andrade, M. C. B. 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science* 271:70-72.
- Andrade, M. C. B. 2003. Risky mate search and male self-sacrifice in redback spiders. *Behavioral Ecology* 14:531-538.
- Aronson, R. 1991. Ecology, paleobiology, and evolutionary constraint in the octopus. *Bulletin of Marine Science* 49:245-255.
- Ayari, A., C. Ghemari, and K. Nasri-Ammar. 2021. Reproductive adaption as a survival strategy to life in an arid environment: The terrestrial crustacean *Hemilepistus reaumurii* as a model. *Zoologischer Anzeiger* 294:10e19.
- Baer, B. 2005. Sexual selection in *Apis* bees. *Apidologie* 36:187-200.
- Barker, I. K., I. Beveridge, A. J. Bradley, and A. K. Lee. 1978. Observations on spontaneous stress-related mortality among males of the dasyurid marsupial *Antechinus stuartii* Macleay. *Australian Journal of Zoology* 26:435-447.
- Barry, T., M. Unwin, J. Malison, and T. Quinn. 2001. Free and total cortisol levels in semelparous and iteroparous chinook salmon. *Journal of Fish Biology* 59:1673-1676.
- Bell, G. 1980. The costs of reproduction and their consequences. *American Naturalist* 116:45-76.
- Bernard, C., G. Silva Santos, J. A. Deere, R. Rodriguez-Caro, P. Capdevila, E. Kusch, S. Gascoigne, J. Jackson, and R. Salguero-Gómez. 2022. MOSAIC: A unified trait database to complement structured population models. *bioRxiv* <https://www.biorxiv.org/content/10.1101/2022.03.09.483599v2>.

920 Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes
 921 sex. *Ecological Monographs* 52:335-351.

922 Boonstra, R., J. M. Barker, J. Castillo, and Q. E. Fletcher. 2007. The role of the stress axis in
 923 life-history adaptations. Pages 139-146 in J. Wolff and P. Sherman, editors. *Rodent*
 924 *societies, an ecological and evolutionary perspective*. University of Chicago Press,
 925 Chicago.

926 Boonstra, R., C. J. McColl, and T. J. Karels. 2001. Reproduction at all costs: The adaptive
 927 stress response of male Arctic ground squirrels. *Ecology* 82:1930-1946.

928 Bosch, I., and M. Slattery. 1999. Costs of extended brood protection in the Antarctic sea star,
 929 *Neosmilaster georgianus* (Echinodermata: Asteroidea). *Marine Biology* 134:449-450.

930 Braithwaite, R. W., and A. K. Lee. 1979. A mammalian example of semelparity. *American*
 931 *Naturalist* 113:151-155.

932 Brown, W. D., and K. L. Barry. 2016. Sexual cannibalism increases male material investment
 933 in offspring: quantifying terminal reproductive effort in a praying mantis. *Proceedings*
 934 *of the Royal Society B-Biological Sciences* 283.

935 Byng, J. W., M. W. Chase, M. J. M. Christenhusz, M. F. Fay, W. S. Judd, D. J. Mabberley,
 936 A. N. Sennikov, D. E. Soltis, P. S. Soltis, P. F. Stevens, B. Briggs, S. Brockington, A.
 937 Chautems, J. C. Clark, J. Conran, E. Haston, M. Moller, M. Moore, R. Olmstead, M.
 938 Perret, L. Skog, J. Smith, D. Tank, M. Vorontsova, A. Weber, and G. Angiosperm
 939 Phylogeny. 2016. An update of the Angiosperm Phylogeny Group classification for the
 940 orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean*
 941 *Society* 181:1-20.

942 Calow, P., and D. Read. 1986. Ontogenetic patterns and phylogenetic trends in freshwater
 943 flatworms (Tricladida); constraint or selection? *Hydrobiologia* 132:263-272.

944 Campton, D. E. 2005. Sperm competition in salmon hatcheries - The need to institutionalize
 945 genetically benign spawning protocols: Response to comment. Transactions of the
 946 American Fisheries Society 134:1495-1498.

947 Casadevall, M., L. Sarra-Alarcon, E. Delgado, and J. Matallanas. 2017. The sexual
 948 segregation of the European eel, *Conger conger* (Linnaeus, 1758) (Anguilliformes,
 949 Congridae) and female semelparity in the northwest Mediterranean. Journal of
 950 Fisheries Research 1:5-14.

951 Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press,
 952 Cambridge, UK.

953 Charnov, E. L., and W. M. Schaffer. 1973. Life history consequences of natural selection-
 954 Cole's result revisited. American Naturalist 107:791-793.

955 Christenson, T., S. Brown, P. Wenzl, E. Hill, and K. Goist. 1985. Mating Behavior of the
 956 golden orb weaving spider, *Nephila clavipes*: I. female receptivity and male courtship.
 957 Journal of Comparative Psychology 99:160-166.

958 Christiansen, J. S., K. Praebel, S. I. Siikavuopio, and J. E. Carscadden. 2008. Facultative
 959 semelparity in capelin *Mallotus villosus* (Osmeridae) - an experimental test of a life
 960 history phenomenon in a sub-arctic fish. Journal of Experimental Marine Biology and
 961 Ecology 360:47-55.

962 Clements, C. F., J. L. Blanchard, K. L. Nash, M. A. Hindell, and A. Ozgul. 2017. Body size
 963 shifts and early warning signals precede the historic collapse of whale stocks. Nature
 964 Ecology & Evolution 1:0188.

965 Clifford, H. 1982. Life cycles of mayflies (Ephemoptera) with special reference to voltinism.
 966 Quaestiones Entomologicae 18:15-90.

967 Cohn, J., and T. Christensen. 1987. Utilization of resources by the male golden orb weaving
 968 spider *Nephila clavipes* (Araneae). 15:185-192.

969 Cohn, J., and T. Christensen. 1988. In defense of *Nephila clavipes*: Postmate guarding by the
970 male golden orb weaving spider. *Journal of Comparative Psychology* 4:319-325.

971 Collett, R. A., A. M. Baker, and D. O. Fisher. 2018. Prey productivity and predictability drive
972 different axes of life-history variation in carnivorous marsupials. *Proceedings of the*
973 *Royal Society B-Biological Sciences* 285.

974 Coulson, T., F. Guinness, J. Pemberton, and T. H. Clutton-Brock. 2004. The demographic
975 consequences of releasing a population of red deer from culling. *Ecology* 85:411–422.

976 Crespi, B. J. 2004. Vicious circles: positive feedback in major evolutionary and ecological
977 transitions. *Trends in Ecology & Evolution* 19:627-633.

978 Crespi, B. J., and R. Teo. 2002. Comparative phylogenetic analysis of the evolution of
979 semelparity and life history in salmonid fishes. *Evolution* 56:1008-1020.

980 Cui, R., T. Medeiros, D. Willemsen, L. N. M. Iasi, G. E. Collier, M. Graef, M. Reichard, and
981 D. R. Valenzano. 2019. Relaxed selection limits lifespan by increasing mutation load.
982 *Cell* 178:385.

983 Cunningham, C., S. Comte, H. McCallum, D. Hamilton, R. Hamede, A. Storfer, T. Hollings,
984 M. Ruiz-Aravena, D. Kerlin, B. Brook, G. Hocking, and M. Jones. 2021. Quantifying
985 25 years of disease-caused declines in Tasmanian devil populations: host density drives
986 spatial pathogen spread. *Ecology Letters* 24:958-969.

987 Deiner, K., J. C. Garza, R. Coey, and D. J. Girman. 2007. Population structure and genetic
988 diversity of trout (*Oncorhynchus mykiss*) above and below natural and man-made
989 barriers in the Russian River, California. *Conservation Genetics* 8:437-454.

990 DeJong, T., and P. Klinkhamer. 1989. Size-dependency of sex-allocation in hermaphroditic,
991 monocarpic plants. *Functional Ecology* 3:201-206.

992 Delph, L. F., and T. L. Ashman. 2006. Trait selection in flowering plants: how does sexual
993 selection contribute? *Integrative and Comparative Biology* 46:465-472.

994 Depczynski, M., and D. Bellwood. 2006. Extremes, plasticity, and invariance in vertebrate
 995 life history traits: insights from coral reef fishes. *Ecology* 87:3119–3127.

996 Deshmukh, U. 2015. Suicidal maternal care (matrphagy) in *Stegodyphus sarasinorum*
 997 (Arachnida: Eresidae). *International Journal of Pharmacology and Biological Sciences*
 998 9:189-192.

999 Diamond, J. M. 1982. Big-bang reproduction and ageing in male marsupial mice. *Nature*
 1000 298:115-116.

1001 Downes, J. 1978. Feeding and mating in the insectivorous Ceratopogoninae (Diptera).
 1002 *Memoirs of the Entomological Society of Canada* 110:1-62.

1003 Drent, R. H., and S. Daan. 1980. The prudent parent- energetic adjustments in avian
 1004 breeding. *Ardea* 68:225-252.

1005 Duffield, K., E. Bowers, S. Sakaluk, and B. Sadd. 2017. A dynamic threshold model for
 1006 terminal investment. *Behavioral Ecology and Sociobiology* 71:185.

1007 Duncan, S. S., and J. L. Williams. 2020. Life history variation in an invasive plant is
 1008 associated with climate and recent colonization of a specialist herbivore. *American*
 1009 *Journal of Botany* 107:1366-1374.

1010 Dunham, A. E., and D. B. Miles. 1985. Patterns of covariation in life history traits of
 1011 squamate reptiles- the effects of size and phylogeny reconsidered. *American Naturalist*
 1012 126:231-257.

1013 Eckhardt, F., P. M. Kappeler, and C. Kraus. 2017. Highly variable lifespan in an annual
 1014 reptile, Labord's chameleon (*Furcifer labordi*). *Scientific Reports* 7.

1015 Edwards, P. D., R. Palme, and R. Boonstra. 2016. Seasonal programming, not competition or
 1016 testosterone, drives stress-axis changes in a partially-semelparous mammal. *Hormones*
 1017 *and Behavior* 85:96-101.

1018 Evans, M. E. K., D. J. Hearn, W. J. Hahn, J. M. Spangle, and D. L. Venable. 2005. Climate
 1019 and life-history evolution in evening primroses (*Oenothera*, Onagraceae): A
 1020 phylogenetic comparative analysis. *Evolution* 59:1914-1927.

1021 Evans, T. 1998. Offspring recognition by mother crab spiders with extreme maternal care.
 1022 *Proceedings of the Royal Society B-Biological Sciences* 265:129-134.

1023 Figueroa, D., G. Macchi, and M. Haimovici. 2009. News about the reproductive ecology of
 1024 the southern conger eel *Conger orbignianus*. *Journal of the Marine Biological*
 1025 *Association of the United Kingdom* 10.1017/S0025315409991135:1-5.

1026 Finch, C. 1994. Latent capacities for gametogenic cycling in the semelparous invertebrate
 1027 *Nereis*. *Proceedings of the National Academy of Sciences of the United States of*
 1028 *America* 91:11769-11770.

1029 Finch, C., and M. Rose. 1995. Hormones and the physiological architecture of life history
 1030 evolution. *Quarterly Review of Biology* 70:1-52.

1031 Fisher, A. M., S. J. Cornell, G. I. Holwell, and T. A. R. Price. 2018. Sexual cannibalism and
 1032 population viability. *Ecology and Evolution* 8:6663-6670.

1033 Fisher, D., and S. Blomberg. 2011. Costs of reproduction and terminal investment by females
 1034 in a semelparous marsupial. *Plos One* 6:e15226.

1035 Fisher, D., C. Dickman, M. Jones, and S. Blomberg. 2013. Sperm competition drives the
 1036 evolution of suicidal reproduction in mammals *Proceedings of the National Academy*
 1037 *of Sciences of the United States of America* 110:1710-17914.

1038 Fisher, D., M. Double, S. Blomberg, M. Jennions, and A. Cockburn. 2006. Post-mating
 1039 sexual selection increases lifetime fitness of polyandrous females in the wild. *Nature*
 1040 444:89-92.

1041 Fisher, D. O., and A. Cockburn. 2006. The large-male advantage in brown antechinuses:
 1042 female choice, male dominance, and delayed male death. *Behavioral Ecology* 17:164-
 1043 171.

1044 Fisher, D. O., I. P. F. Owens, and C. N. Johnson. 2001. The ecological basis of life history
 1045 variation in marsupials. *Ecology* 82:3531–3540.

1046 Fiz, O., V. Valcarcel, and P. Vargas. 2002. Phylogenetic position of Mediterranean Astereae
 1047 and character evolution of daisies (*Bellis*, Asteraceae) inferred from nrDNA ITS
 1048 sequences. *Molecular phylogenetics and evolution* 25:157-171.

1049 Foellmer, M. W., and D. J. Fairbairn. 2003. Spontaneous male death during copulation in an
 1050 orb-weaving spider. *Proceedings of the Royal Society B-Biological Sciences* 270:S183-
 1051 S185.

1052 Forster, L. M. 1992. The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti*
 1053 Thorell (Araneae: Theridiidae) the Australian redback spider. *Australian Journal of*
 1054 *Zoology* 40:1-11.

1055 Friedman, J. 2020. The evolution of annual and perennial plant life histories: ecological
 1056 correlates and genetic mechanisms. *Annual Review of Ecology, Evolution, and*
 1057 *Systematics* 51:461-481.

1058 Fromhage, L., M. A. Elgar, and J. M. Schneider. 2005. Faithful without care: The evolution
 1059 of monogyny. *Evolution* 59:1400-1405.

1060 Futami, K., and S. Akimoto. 2005. Facultative second oviposition as an adaptation to egg loss
 1061 in a semelparous crab spider. *Ethology* 111:1126—1138.

1062 Gaillard, J. M., D. Pontier, D. Allaine, J. D. Lebreton, J. Trouvilliez, and J. Clobert. 1989. An
 1063 analysis of demographic tactics in birds and mammals. *Oikos* 56:59-76.

1064 Grearson, A., A. Dugan, T. Sakmar, D. Sivitilli, D. Gire, R. Caldwell, C. Niell, G. Dölen, Z.
1065 Wang, and B. Grasse. 2021. The lesser Pacific striped octopus, *Octopus chierchiae*: an
1066 emerging laboratory model *Frontiers in Marine Science* 8:753483

1067 Grosberg, R. 1988. Life history variation within a population of the colonial ascidian
1068 *Botryllus schlosseri*. 1. Genetic and environmental control of seasonal variation.
1069 *Evolution* 42:900-920.

1070 Guillet, S., and M. Vancassel. 2001. Dermapteran life-history evolution and phylogeny with
1071 special reference to the Forficulidae family. *Evolutionary Ecology Research* 3:441–
1072 447.

1073 Hautekeete, N. C., Y. Piquot, and H. Van Dijk. 2001. Investment in survival and reproduction
1074 along a semelparity-iteroparity gradient in the *Beta* species complex. *Journal of*
1075 *Evolutionary Biology* 14:795-804.

1076 Healy, K., T. Ezard, O. Jones, R. Salguero-Gómez, and Y. Buckley. 2019. Animal life history
1077 is shaped by the pace of life and the distribution of age-specific mortality and
1078 reproduction. *Nature Ecology and Evolution* 3:1217.

1079 Hendry, A. P., Y. E. Morbey, O. K. Berg, and J. K. Wenburg. 2004. Adaptive variation in
1080 senescence: reproductive lifespan in a wild salmon population. *Proceedings of the*
1081 *Royal Society of London Series B-Biological Sciences* 271:259-266.

1082 Herberstein, M. E., A. C. Gaskett, J. M. Schneider, N. G. F. Vella, and M. A. Elgar. 2005.
1083 Limits to male copulation frequency: Sexual cannibalism and sterility in St Andrew's
1084 cross spiders (Araneae, Araneidae). *Ethology* 111:1050-1061.

1085 Hironaka, M., L. Filippi, S. Nomakuchi, and T. Hariyama. 2007. Guarding behaviour against
1086 intraspecific kleptoparasites in the subsocial shield bug, *Parastrachia japonensis*
1087 (Heteroptera: Parastrachiidae). *Behaviour* 145:815-827.

1088 Hironaka, Y., and H. Abe. 2012. Nesting habits of the Japanese foliage spider,
 1089 *Cheiracanthium japonicum* (Araneae: Miturgidae): host plant preference based on the
 1090 physical traits of plant leaves. *Journal of Natural History* 46:43-44.
 1091 Holldobler, B. 1976. Behavioral ecology of mating in harvester ants (Hymenoptera-
 1092 Formicidae- Pogonomyrex). *Behavioral Ecology and Sociobiology* 1:405-423.
 1093 Hruska, K., S. Hinch, M. Healey, D. Patterson, S. Larsson, and A. Farrell. 2010. Influences of
 1094 sex and activity level on physiological changes in Individual adult sockeye salmon
 1095 during rapid senescence. *Physiological and Biochemical Zoology* 83:663–676.
 1096 Hughes, P. W. 2017. Between semelparity and iteroparity: Empirical evidence for a
 1097 continuum of modes of parity. *Ecology and Evolution* 7:8232–8261.
 1098 Hurd, L. 1989. The importance of late season flowers to the fitness of an insect predator,
 1099 *Tenodera sinensis* Saussure (Orthoptera: Mantidae) in an old field community.
 1100 *Entomologist* 108:223-228.
 1101 Huse, G. 1998. Sex-specific life history strategies in capelin (*Mallotus villosus*)? *Canadian*
 1102 *Journal of Fisheries and Aquatic Science* 55:631-638.
 1103 Ibanez, C., M. Díaz-Santana-Iturrios, D. Lopez-Cordova, S. Carrasco, M. Pardo-Gandarillas,
 1104 F. Rocha, and E. Vidal. 2021. A phylogenetic approach to understand the evolution of
 1105 reproduction in coleoid cephalopods. *Molecular phylogenetics and evolution*
 1106 155:106972.
 1107 Iguchi, K., and Y. Tsukamoto. 2001. Semelparous or iteroparous: resource allocation tactics
 1108 in the ayu, an osmeroid fish. *Journal of Fish Biology* 58:520–528.
 1109 Janzen, D. 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and*
 1110 *Systematics* 7:347-391.

1111 Jellyman, D. J. 2021. An enigma: how can freshwater eels (*Anguilla* spp.) be such a
 1112 successful genus yet be universally threatened? Reviews in Fish Biology and Fisheries
 1113 8:s11160-02109658.

1114 Jiguet, F., A. Gadot, R. Julliard, S. Newson, and D. Couvet. 2007. Climate envelope, life
 1115 history traits and the resilience of birds facing global change. Global Change Biology
 1116 13:1672-1684.

1117 Jonsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in
 1118 reproduction. Oikos 78:57-66.

1119 Junghanns, A., C. Holm, M. Schou, A. Sorensen, G. Uhl, and T. Bilde. 2017. Extreme
 1120 allomaternal care and unequal task participation by unmated females in a cooperatively
 1121 breeding spider. Animal Behaviour 132:101e107.

1122 Karsten, K. B., L. N. Andriamandimbiarisoa, S. F. Fox, and C. J. Raxworthy. 2008. A unique
 1123 life history among tetrapods: An annual chameleon living mostly as an egg.
 1124 Proceedings of the National Academy of Sciences of the United States of America
 1125 105:8980-8984.

1126 Keeley, J. E., and W. J. Bond. 1999. Mast flowering and semelparity in bamboos: The
 1127 bamboo fire cycle hypothesis. American Naturalist 154:383-391.

1128 Kern, C. C., and D. Gems. 2022. Semelparous death as one element of iteroparous aging
 1129 gone large. Frontiers in Genetics 13:880343.

1130 Kim, E., and K. Donohue. 2012. The effect of plant architecture on drought resistance:
 1131 implications for the evolution of semelparity in *Erysimum capitatum*. Functional
 1132 Ecology 26:294–303.

1133 Kim, K. W., C. Roland, and A. Horel. 2000. Functional value of matriphagy in the spider
 1134 *Amaurobius ferox*. Ethology 106:729-742.

1135 Kindsvater, H. K., D. C. Braun, S. P. Otto, and J. D. Reynolds. 2016. Costs of reproduction
 1136 can explain the correlated evolution of semelparity and egg size: theory and a test with
 1137 salmon. *Ecology Letters* 19:687-696.

1138 Kirkwood, T. B. L. 1977. Evolution of aging. *Nature* 270:301-304.

1139 Knoflach, B., and S. Benjamin. 2003. Mating without sexual cannibalism in *Tidarren*
 1140 *Sisyphoides* (Araneae, Theridiidae). *Journal of Arachnology* 31:445-448.

1141 Knoflach, B., and A. Van Harten. 2000. Palpal loss, single palp copulation and obligatory
 1142 mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae).
 1143 *Journal of Natural History* 34:1639-1659.

1144 Knoflach, B., and A. van Harten. 2001. *Tidarren argo* sp nov (Araneae : Theridiidae) and its
 1145 exceptional copulatory behaviour: emasculation, male palpal organ as a mating plug
 1146 and sexual cannibalism. *Journal of Zoology* 254:449-459.

1147 Kohno, K. 1997. Possible influences of habitat characteristics on the evolution of semelparity
 1148 and cannibalism in the hump earwig *Anechura harmandi*. *Research in Population*
 1149 *Ecology* 39:11-16.

1150 Kuntner, M., S. Kralj-Fiser, J. M. Schneider, and D. Li. 2009. Mate plugging via genital
 1151 mutilation in nephilid spiders: an evolutionary hypothesis. *Journal of Zoology* 277:257-
 1152 266.

1153 Lachish, S., H. McCallum, and M. Jones. 2009. Demography, disease and the devil: life-
 1154 history changes in a disease-affected population of Tasmanian devils (*Sarcophilus*
 1155 *harrisii*). *Journal of Animal Ecology* 78:427-436.

1156 Lankinen, A., S. Hydbom, and M. Strandh. 2017. Sexually antagonistic evolution caused by
 1157 male–male competition in the pistil. *Evolution* 71:2359–2369.

1158 Larsen, L., and S. Dufour. 1993. Growth, reproduction and death in lampreys and eels. Pages
 1159 72-105 in J. Rankin and F. Jensen, editors. Fish Ecophysiology. Chapman & Hall,
 1160 London.

1161 Lazenby, B. T., M. W. Tobler, W. E. Brown, C. E. Hawkins, G. J. Hocking, F. Hume, S.
 1162 Huxtable, P. Iles, M. E. Jones, C. Lawrence, S. Thalmann, P. Wise, H. Williams, S.
 1163 Fox, and D. Pemberton. 2018. Density trends and demographic signals uncover the
 1164 long-term impact of transmissible cancer in Tasmanian devils. Journal of Applied
 1165 Ecology 55:1368-1379.

1166 Lee, Q. Q., J. Oh, S. Kralj-Fiser, M. Kuntner, and D. Q. Li. 2012. Emasculation: gloves-off
 1167 strategy enhances eunuch spider endurance. Biology Letters 8:733-735.

1168 LeGrand, R., and D. Morse. 2000. Factors driving extreme sexual size dimorphism of a sit-
 1169 and-wait predator under low density. Biological Journal of the Linnean Society 71:643–
 1170 664.

1171 Leiner, N. O., E. Z. F. Setz, and W. R. Silva. 2008. Semelparity and factors affecting the
 1172 reproductive activity of the Brazilian slender opossum (*Marmosops paulensis*) in
 1173 southeastern Brazil. Journal of Mammalogy 89:153-158.

1174 Lopes, G. P., and N. O. Leiner. 2015. Semelparity in a population of *Gracilinanus agilis*
 1175 (Didelphimorphia: Didelphidae) inhabiting the Brazilian cerrado. Mammalian Biology
 1176 80:1-6.

1177 Macqueen, D. J., and I. A. Johnston. 2014. A well-constrained estimate for the timing of the
 1178 salmonid whole genome duplication reveals major decoupling from species
 1179 diversification. Proceedings of the Royal Society B-Biological Sciences 281.

1180 Maltby, L., and P. Calow. 1986. Intraspecific life-history variation in *Erpobdella octoculata*
 1181 (Hirudinea: Erpobdellidae). II. Testing theory on the evolution of semelparity and
 1182 iteroparity Journal of Animal Ecology 55:739-750.

1183 Martins, E. G., V. Bonato, C. Q. da-Silva, and S. F. dos Reis. 2006. Seasonality in
 1184 reproduction, age structure and density of the gracile mouse opossum *Gracilinanus*
 1185 *microtarsus* (Marsupialia : Didelphidae) in a Brazilian cerrado. Journal of Tropical
 1186 Ecology 22:461-468.

1187 McQueen, D. 1978. Field studies of growth, reproduction, and mortality in the burrowing
 1188 wolf spider *Geolycosa domifex* (Hancock). Canadian Journal of Zoology 56:2037-2049.

1189 Medawar, P. 1952. An unsolved problem of Biology. HK Lewis, London.

1190 Metcalf, J. C., K. E. Rose, and M. Rees. 2003. Evolutionary demography of monocarpic
 1191 perennials. Trends in Ecology and Evolution 18:471-480.

1192 Michalik, P., and C. C. Rittschof. 2011. A comparative analysis of the morphology and
 1193 evolution of permanent sperm depletion in spiders. Plos One 6.

1194 Mills, H. R., and R. Bencini. 2000. New evidence for facultative male die-off in island
 1195 populations of dibblers, *Parantechinus apicalis*. Australian Journal of Zoology 48:501-
 1196 510.

1197 Minnaar, C., B. Anderson, M. deJager, and J. Karron. 2019. Plant–pollinator interactions
 1198 along the pathway to paternity. Annals of Botany 123:225–245.

1199 Monnin, T. 1998. Monogyny and regulation of worker mating in the queenless ant
 1200 *Dinoponera quadriceps*. Animal Behaviour 55:299-306.

1201 Monroe, J. G., B. Gill, K. G. Turner, and J. K. McKay. 2019. Drought regimens predict life
 1202 history strategies in *Heliophila*. New Phytologist 223:2054-2062.

1203 Mora, C., D. P. Tittensor, S. Adl, A. G. B. Simpson, and B. Worm. 2011. How many species
 1204 are there on earth and in the ocean? Plos Biology 9.

1205 Morse, D. 1994. Numbers of broods produced by the crab spider *Misumena vatia* (Araneae,
 1206 Thomisidae). Journal of Arachnology 22:195-199.

1207 Morse, D. 2012. Reproductive output of a female crab spider: the impacts of mating failure,
 1208 natural enemies, and resource availability. *Entomologia Experimentalis Et Applicata*
 1209 146:141–148.

1210 Morse, D., and E. Stephens. 1996. The consequences of adult foraging success on the
 1211 components of lifetime fitness in a semelparous, sit and wait predator. *Evolutionary*
 1212 *Ecology* 10:361-373.

1213 Nicholson, J. W. 1922. Note on the distribution and habit of *Dendrocalamus strictus* and
 1214 *Bambusa arundinacea* in Orissa. *Indian Forest* 48:425-428.

1215 Nobel, P. S. 1977. Water relations of flowering *Agave deserti*. *Botanical Gazette* 138:1-6.

1216 Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Bratney, B. Ernande, and U.
 1217 Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse
 1218 of northern cod. *Nature* 428:932–935.

1219 Paige, K., and T. Whitham. 1987. Flexible life history traits: shifts by scarlet gilia in response
 1220 to pollinator abundance. *Ecology* 68:1691-1695.

1221 Pandian, T. J. 2018. Reproduction and development in Echinodermata and Prochordata. CRC
 1222 Press Boca Raton, Florida, United States.

1223 Paniw, M., A. Ozgul, and R. Salguero-Gómez. 2018. Interactive life-history traits predict
 1224 sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters* 21:275-
 1225 286.

1226 Pavard, S., C. J. E. Metcalf, and E. Heyer. 2008. Senescence of reproduction may explain
 1227 adaptive menopause in humans: A test of the "Mother" hypothesis. *American Journal*
 1228 *of Physical Anthropology* 136:194-203.

1229 Petry, W. K., J. D. Soule, A. M. Iler, A. Chicas-Mosier, D. W. Inouye, T. E. X. Miller, and K.
 1230 A. Mooney. 2016. Sex-specific responses to climate change in plants alter population
 1231 sex ratio and performance. *Science* 353:69-71.

1232 Pine, R. 1994. Sex and Death. Australian Natural History 24:4.

1233 Pitcher, T. E., P. O. Dunn, and L. A. Whittingham. 2005. Sperm competition and the
 1234 evolution of testes size in birds. Journal of Evolutionary Biology 18:557-567.

1235 Poppenwimer, T., I. Mayrose, and N. DeMalach. 2022. Revising the global biogeography of
 1236 plant life cycles. bioRxiv
 1237 <https://www.biorxiv.org/content/10.1101/2022.09.13.507878v1>.

1238 Ramos, M., D. J. Irschick, and T. E. Christenson. 2004. Overcoming an evolutionary conflict:
 1239 Removal of a reproductive organ greatly increases locomotor performance. Proceedings
 1240 of the National Academy of Sciences of the United States of America 101:4883-4887.

1241 Rees, M., D. Z. Childs, and S. P. Ellner. 2014. Building integral projection models: a user's
 1242 guide. Journal of Animal Ecology 83:528-545.

1243 Reichard, M., and M. Polacik. 2019. *Nothobranchius furzeri*, an 'instant' fish from an
 1244 ephemeral habitat Elife 8:e41548.

1245 Reznick, D., M. Bryant, and D. Holmes. 2006. The evolution of senescence and post-
 1246 reproductive lifespan in guppies (*Poecilia reticulata*). Plos Biology 4:136-143.

1247 Righton, D., K. Aarestrup, D. Jellyman, P. Sebert, G. van den Thillart, and K. Tsukamoto.
 1248 2012. The *Anguilla* spp. migration problem: 40 million years of evolution and two
 1249 millennia of speculation. Journal of Fish Biology 81:365-386.

1250 Robison, B., B. Seibel, and J. Drazen. 2014. Deep sea octopus (*Graneledone boreopacifica*)
 1251 conducts the longest-known egg-brooding period of any animal PLoS ONE 9:e103437.

1252 Rocha, F., A. Guerra, and A. Gonzalez. 2001. A review of reproductive strategies in
 1253 cephalopods. Biological Reviews 76:291-304.

1254 Roff, D. A. 1992. The evolution of life histories. Chapman and Hall, New York.

1255 Römer, G., J. Dahlgren, R. Salguero-Gómez, I. Stott, and O. Jones. 2022. Plant demographic
 1256 knowledge is biased towards short-term studies of temperate-region herbaceous
 1257 perennials. *bioRxiv* <https://doi.org/10.1101/2021.04.25.441327>

1258 Ronce, O., and D. Promislow. 2010. Kin competition, natal dispersal and the moulding of
 1259 senescence by natural selection. *Proceedings of the Royal Society B-Biological*
 1260 *Sciences* 277:3659–3667.

1261 Roper, M., P. Capdevila, and R. Salguero-Gomez. 2021. Senescence: why and where
 1262 selection gradients might not decline with age. *Proceedings of the Royal Society B-*
 1263 *Biological Sciences* 288.

1264 Salguero-Gomez, R. 2017. Applications of the fast-slow continuum and reproductive strategy
 1265 framework of plant life histories. *New Phytologist* 213:1618-1624.

1266 Salguero-Gomez, R., O. R. Jones, E. Jongejans, S. P. Blomberg, D. J. Hodgson, C. Mbeau-
 1267 Ache, P. A. Zuidema, H. de Kroon, and Y. M. Buckley. 2016. Fast-slow continuum and
 1268 reproductive strategies structure plant life-history variation worldwide. *Proceedings of*
 1269 *the National Academy of Sciences of the United States of America* 113:230-235.

1270 Salguero-Gomez, R., R. P. Shefferson, and M. J. Hutchings. 2013. Plants do not count... or
 1271 do they? New perspectives on the universality of senescence. *Journal of Ecology*
 1272 101:545-554.

1273 Salomon, M., E. Aflalo, M. Col, and Y. Lubin. 2015. Dramatic histological changes
 1274 preceding suicidal maternal care in the subsocial spider *Stegodyphus lineatus* (Araneae:
 1275 Eresidae). *Journal of Arachnology* 43:77-85.

1276 Salomon, M., J. Schneider, and Y. Lubin. 2005. Maternal investment in a spider with suicidal
 1277 maternal care, *Stegodyphus lineatus* (Araneae, Eresidae). *Oikos* 109:614-622.

1278 Sasaki, T., and O. Iwahashi. 1995. Sexual cannibalism in an orb-weaving spider *Argiope*
 1279 *aemula*. 49 *Animal Behaviour*:1119-1121.

1280 Sato, N., S.-I. Tsuda, M. N. E. Alam, T. Sasanami, Y. Iwata, S. Kusama, O. Inamura, M.-a.
 1281 Yoshida, and N. Hirohashi. 2020. Rare polyandry and common monogamy in the
 1282 firefly squid, *Watasenia scintillans*. Scientific Reports 10.
 1283 Schaffer, W., and M. Gadgil. 1975. Selection for optimal life histories in plants. Pages 142-
 1284 157 in M. Cody and J. Diamond, editors. Ecology and evolution of communities.
 1285 Belknap Press, Cambridge, Massachusetts.
 1286 Schaffer, W., and M. Schaffer. 1979. The adaptive significance of variations in reproductive
 1287 habit in the Agavaceae II: pollinator foraging behavior and selection for increased
 1288 reproductive expenditure. Ecology 60:1051-1069.
 1289 Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. American
 1290 Naturalist 108:783-790.
 1291 Schneider, J. M., and Y. Lubin. 1997. Does high adult mortality explain semelparity in the
 1292 spider *Stegodyphus lineatus* (Eresidae)? Oikos 79:92-100.
 1293 Schneider, J. M., and P. Michalik. 2011. One-shot genitalia are not an evolutionary dead end:
 1294 regained male polygamy in a sperm limited spider species. BMC Evolutionary Biology
 1295 11.
 1296 Schwartz, S. K., W. E. Wagner, Jr., and E. A. Hebets. 2014. Obligate male death and sexual
 1297 cannibalism in dark fishing spiders. Animal Behaviour 93:151-156.
 1298 Schwartz, S. K., W. E. Wagner, Jr., and E. A. Hebets. 2016. Males can benefit from sexual
 1299 cannibalism facilitated by self-sacrifice. Current Biology 26:2794-2799.
 1300 Shuster, S. 1991. Changes in female anatomy associated with the reproductive moult in
 1301 *Paracerceis sculpta*, a semelparous isopod crustacean. Journal of Zoology 225:365-
 1302 379.
 1303 Silvertown, J. 1983. Why are biennials sometimes not so few? American Naturalist 121:448-
 1304 453.

1305 Silvertown, J. 1996. Are sub-alpine firs evolving towards semelparity? *Evolutionary Ecology*
1306 10:77-80.

1307 Smith, F. A., and E. L. Charnov. 2001. Fitness trade-offs select for semelparous reproduction
1308 in an extreme environment. *Evolutionary Ecology Research* 3:595-602.

1309 Soltis, D. E., M. E. Mort, M. Latvis, E. V. Mavrodiev, B. C. O'Meara, P. S. Soltis, J. G.
1310 Burleigh, and R. R. de Casas. 2013. Phylogenetic relationships and character evolution
1311 analysis of saxifragales using a supermatrix approach. *American Journal of Botany*
1312 100:916-929.

1313 Soulsbury, C. D. 2010. Genetic patterns of paternity and testes size in mammals. *Plos One*
1314 5:e9581.

1315 Stearns, S. C. 1976. Life History tactics: a review of the ideas. *Quarterly Review of Biology*
1316 51:3-47.

1317 Stebbins, G. 1950. *Variation and Evolution in Plants*. Columbia Uni Press, New York.

1318 Suzuki, S., M. Kitamura, and K. Matsubayashi. 2005. Matriphagy in the hump earwig,
1319 *Anechura harmandi* (Dermaptera : Forficulidae), increases the survival rates of the
1320 offspring. *Journal of Ethology* 23:211-213.

1321 Tachikawa, S. S., C.W. . 1985. Biology of *Parastrachia japonensis* (Hemiptera:
1322 Pentatomidae) *Annals of the Entomological Society of America* 78:387-397.

1323 Taggart, D. A., J. Johnson, and P. D. Templesmith. 1993. Testicular and epididymal
1324 development in the brown marsupial mouse, *Antechinus stuartii* (Dasyuridae,
1325 Marsupialia). *Anatomy and Embryology* 188:87-100.

1326 Taggart, D. A., and P. D. Templesmith. 1991. Transport and storage of spermatozoa in the
1327 female reproductive tract of the brown marsupial mouse, *Antechinus stuartii*
1328 (Dasyuridae). *Journal of Reproduction and Fertility* 93:97-110.

1329 Takada, T. 1995. Evolution of semelparous and iteroparous perennial plants- comparison
1330 between the density-independent and density-dependent dynamics. Journal of
1331 Theoretical Biology 173:51-60.

1332 Tizo-Pedroso, E., and K. Del-Claro. 2005. Matriphagy in the neotropical pseudoscorpion
1333 *Paratemnoides nidificator* (Balzan 1888) (Atemnidae). Journal of Arachnology 33:873-
1334 877.

1335 Toyama, M. 1999. Adaptive advantages of maternal care and matriphagy in a foliage spider,
1336 *Chiracanthium japonicum* (Araneae : Clubionidae). Journal of Ethology 17:33-39.

1337 Traill, L. W., S. Schindler, and T. Coulson. 2014. Demography, not inheritance, drives
1338 phenotypic change in hunted bighorn sheep. Proceedings of the National Academy of
1339 Sciences of the United States of America 111:13223-13228.

1340 Tripathi, R., A. Jangid, M. Siliwal, and S. Dutta. 2020. The first report of matriphagy in
1341 *Stegodyphus pacificus* Pocock 1900. Acta Arachnologica 69:17–21.

1342 Trumbo, S. T. 2013. Maternal care, iteroparity and the evolution of social behavior: a critique
1343 of the semelparity hypothesis. Evolutionary Biology 40:613-626.

1344 Tsukamoto, K., S. Chow, T. Otake, H. Kurogi, N. Mochioka, M. Miller, J. Aoyama, S.
1345 Kimura, S. Watanabe, T. Yoshinaga, A. Shinoda, M. Kuroki, M. Oya, T. Watanabe, K.
1346 Hata, S. Ijiri, Y. Kazeto, K. Nomura, and H. Tanaka. 2011. Oceanic spawning ecology
1347 of freshwater eels in the western north Pacific. Nature Communications 2:179 doi:
1348 110.1038/ncomms1174.

1349 Tuljapurkar, S., J.M. Gaillard, and T. Coulson. 2009a. From stochastic environments to life
1350 histories and back. Philosophical Transactions of the Royal Society B-Biological
1351 Sciences 364:1499-1509.

1352 Unwin, M., M. Kinnison, and T. Quinn. 1999. Exceptions to semelparity: postmaturation
 1353 survival, morphology, and energetics of male chinook salmon (*Oncorhynchus*
 1354 *tshawytscha*). Canadian Journal of Fisheries and Aquatic Science 56:1172–1181.

1355 Waddell, J., and W. Crampton. 2022. Reproductive effort and terminal investment in a
 1356 multispecies assemblage of Amazon electric fish. Ecological Monographs 92:e1499.

1357 Wang, Z., and C. Ragsdale. 2018. Multiple optic gland signaling pathways implicated in
 1358 octopus maternal behaviors and death. Journal of Experimental Biology
 1359 221:jeb185751.

1360 Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence.
 1361 Evolution 11:398–411.

1362 Williams, G. C. 1966. Natural selection, costs of reproduction, and a refinement of Lack's
 1363 principle. American Naturalist 100:687-690.

1364 Wodinsky, J. 1977. Hormonal inhibition of feeding and death in Octopus: control by optic
 1365 gland secretion. Science 198:948-951.

1366 Woollhead, A., and P. Calow. 1979. Energy-partitioning strategies during egg production in
 1367 semelparous and iteroparous Triclad. Journal of Animal Ecology 48:491-499.

1368 Young, T. 1990. Evolution of semelparity in Mount Kenya lobelias. Evolutionary Ecology
 1369 4:157-171.

1370 Young, T. P., and C. K. Augspurger. 1991. Ecology and evolution of long-lived semelparous
 1371 plants. Trends in Ecology & Evolution 6:285-289.

1372

1373

Figure captions

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

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

Figures

Figure 1

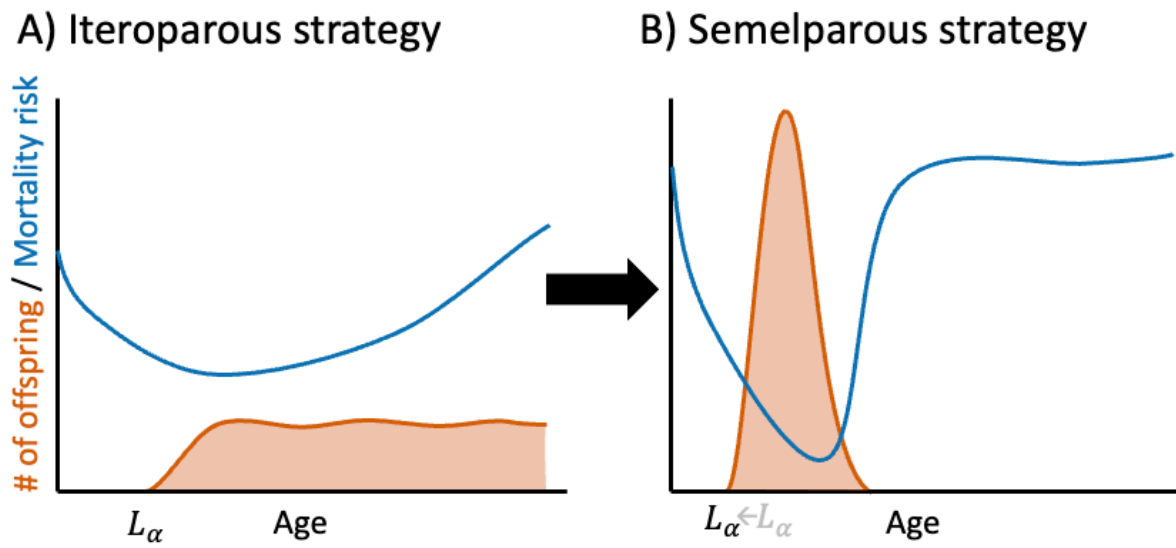
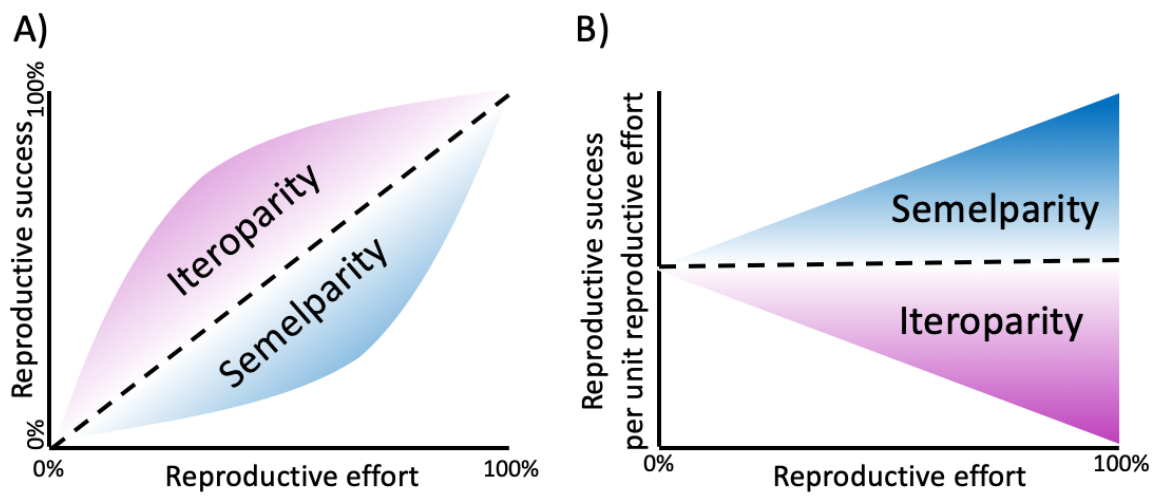


Figure 2



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

1409

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 matrophagy	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 matrophagy have higher mass at dispersal, and higher survival. In experimentally reduced broods, female mass loss per day was low and matrophagy occurred very late or not at all.	(Salomon et al. 2005, Junghans 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 matrophagy, investment in guarding exposing female to predation	Female guarding in enclosed sheet web tube followed by matrophagy. 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 matrophagy 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 matrophagy	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 matrophagy	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 sphaeromatidae	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

Organism	Driver- why lethal reproductive effort may confer greater fitness than iteroparity	Proximate cause of death - reproductive effort mechanism that kills individuals	Explanation	Ref
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, Macqu een and Johnsto n 2014, Kindsv ater 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)

<i>Neotoma lepida</i> Desert woodrat Mammal Family Cricetidae	Much higher adult mortality than juvenile mortality in hot locations (Death Valley USA) and years, due to overheating of large individuals	Females expose themselves to overheating when they invest in high fecundity (body size-litter size correlation). Overheating	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	(Smith and Charnov 2001)
--	--	---	---	--------------------------

1422

1423 **Table S4.** Female vertebrates with obligate semelparity- cannot ovulate more than once.

1424

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>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

Organism	Driver- why lethal reproductive effort may confer greater fitness than iteroparity	Proximate cause of death - reproductive effort mechanism that kills individuals	Explanation	Ref
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	(Haute keete 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>Bellium minus, Bellis annua, and 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

Organism	Driver- why lethal reproductive effort may confer greater fitness than iteroparity	Proximate cause of death - reproductive effort mechanism that kills individuals	Explanation	Ref
<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

Organism	Driver- why lethal reproductive effort may confer greater fitness than iteroparity	Proximate cause of death - reproductive effort mechanism that kills individuals	Explanation	Ref
<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

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>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 oval</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 is 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

1443

Organism	Driver- why lethal reproductive effort may confer greater fitness than iteroparity	Proximate cause of death - reproductive effort mechanism that kills individuals	Explanation	Ref
<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.	(Karsenti 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

chinook, coho, sockeye, chum, pink salmon Fish Family Salmonidae		free corticosteroid level increases ~60-fold in spawning males due to loss of corticosteroid binding globulin. Energy depletion and tissue investment in fighting & mate- guarding	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	Teo 2002, Crespi 2004, Hruska et al. 2010, Macqu een and Johnsto n 2014, Kindsv ater et al. 2016)
---	--	---	--	---

1444

1445 **Table S10.** Male vertebrates with obligate semelparity- incapable of further spermatogenesis

1446

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 Dufoir 1993)

1447