2   **TITLE**

Between semelparity and iteroparity: empirical evidence for a continuum of modes of

4   parity

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8   **AUTHOR**

P. William Hughes
10   Max Planck Institute for Plant Breeding Research
Carl-von-Linné-Weg 10
12   50829 Köln
Email: whughes@mpipz.mpg.de
14

ABSTRACT

16   The number of times an organism reproduces (i.e. its mode of parity) is a

fundamental life-history character, and evolutionary and ecological models that compare

18   the relative fitness of strategies are common in life history theory and theoretical biology.

Despite the success of mathematical models designed to compare intrinsic rates of

20   increase between annual-semelparous and perennial-iteroparous reproductive schedules,

there is widespread evidence that variation in reproductive allocation among semelparous

22   and iteroparous organisms alike is continuous. This paper reviews the ecological and

molecular evidence for the continuity and plasticity of modes of parity—that is, the idea

24   that annual-semelparous and perennial-iteroparous life histories are better understood as

endpoints along a continuum of possible strategies. I conclude that parity should be

26   understood as a continuum of different modes of parity, which differ by the degree to

which they disperse or concentrate reproductive effort in time. I further argue that there

28   are three main implications of this conclusion: (1) That seasonality should not be

conflated with parity; (2) that mathematical models purporting to explain the evolution of

30   semelparous life histories from iteroparous ones (or vice versa) should not assume that

organisms can only display either an annual-semelparous life history or a perennial-

32   iteroparous one; and (3) that evolutionary ecologists should examine the physiological or

molecular basis of traits underlying different modes of parity, in order to obtain a general

34   understanding of how different life history strategies can evolve from one another.

KEY WORDS

36   Parity; semelparity; iteroparity; life history; reproduction; phenology; annual; perennial

CONTENTS

I. INTRODUCTION

58

Semelparity (and the related botanical term "monocarpy") describes the life

60   history defined by a single, highly fecund bout of reproduction, and can be contrasted

with iteroparity ("polycarpy"), the life history defined by repeated (i.e. "iterative") bouts

62   of reproduction throughout life. Identifying the reasons why organisms adopt either mode

of parity is one of life history theory's oldest problems, having been considered by both

64   Aristotle (History of Animals, BkIX, 622 1-30, trans. Thompson, 1907) and Linnaeus

(Linnaeus, 1744). In contemporary evolutionary ecology, this problem has been

66   formalized by age-structured demographic models that seek to explain the eco-

evolutionary dynamics of reproductive patterns by comparing the intrinsic rates of

68   increase of reproductive strategies (Cole, 1954; Bryant, 1971; Charnov and Schaffer,

1973; Young, 1981; Omielan, 1991; Su and Peterman, 2012; Javoiš, 2013; Vaupel et al.,

70   2013; Cushing, 2015). In such models, two modes of parity are considered, classified by

whether they express all reproductive effort in a single year (semelparity), or in more than

72   one (iteroparity). I refer to this simplified conception as the "discrete conception of

parity". The main advantage of the discrete conception of parity is its analytical

74   simplicity; given population growth data, intrinsic rates of increase can be easily

computed and directly compared. Some intraspecific comparisons between

76   phenotypically similar semelparous and iteroparous congeners conform to the predictions

of demographic models based on the discrete conception of parity (e.g. Fritz et al., 1982;

78   Young, 1984, 1990; Iguchi and Tsukamoto, 2001).

However, in this review I will argue that despite the modest successes—both

80   theoretical and empirical—of evolutionary explanations rooted in the discrete conception of parity, sufficient evidence has been accumulated to make it clear that, like many other

82   life-history traits, parity is a continuous variable, and that semelparity and iteroparity are the endpoints of a continuum of possible strategies that define the distribution of

84   reproductive effort through time, rather than simple alternatives describing whether an organism fatally reproduces in a given year or not. On this account, semelparity can be

86   understood as the strategy defined by concentrating reproductive effort in time, and iteroparity as the strategy defined by distributing reproductive effort over longer

88   timescales. I refer to this idea hereafter as the "continuous conception of parity". It is important to note that the continuous conception of parity should not be conflated with

90   the related terms "annuality" and "perenniality". These terms specify strategies defined by the "digitization" of reproduction in response to seasonal effects supervening on the

92   process of reproduction, rather than describing how concentrated reproductive effort is in time. This distinction is further discussed later.

94   The idea that parity itself is continuous and not discrete is not new (see: Hughes and Simons, 2014c; Kirkendall and Stenseth, 1985; Unwin, Kinnison and Quinn, 1999;

96   Roff, 1992), but to date no systematic exposition of the empirical evidence supporting the different conceptions of parity has yet been undertaken. Furthermore, evolutionary

98   explanations of life-history differences between clades with differing modes of parity continue to rely on the discrete conception of parity (e.g. Lopes and Leiner, 2015), and

100   mathematical models based on the formalization of this assumption continue to be produced (e.g. Benton and Grant, 1999, Davydova et al., 2005; Vaupel et al., 2013).

102   However, because of the ubiquity of evolutionary transitions from iteroparity to

semelparity (Table 1), understanding parity as a continuous trait is important for

104   understanding the underlying eco-evolutionary dynamics that affect the fitness of life-

history strategies.

106   In this review I begin by reviewing the development of both the discrete and

continuous conceptions of parity as evolutionary hypotheses and/or models. Next, I

108   review empirical work that highlights the existence of natural variation in reproduction

along a semelparity-iteroparity continuum, focusing on three distinct strategies:

110   facultative iteroparity, facultative semelparity, and phenotypically plastic parity. I

conclude by exploring the implications of the continuous conception of parity for: (1) the

112   study of seasonality as a "digitization" of reproduction, (2) the process of mathematically

modelling life-history optimization, and (3) the study of the molecular regulation of

114   reproductive traits linked to parity.

116   **II. The Discrete Conception of Parity**

(1) 'Cole's Paradox' and the development of the discrete conception of parity

118   Although the first mathematical model of the intrinsic rate of increase of annual

plants was constructed by Linnaeus (1744), Lamont Cole (1954) was the first to

120   categorize life histories into dichotomous "semelparous" and "iteroparous" groups: a

semelparous organism is one that "dies upon producing seed" and therefore "potential

122   population growth may be considered on the assumption that generations do not overlap"

(p. 109), while iteroparous organisms include a variety of cases, from those where "only

124   two or three litters of young are produced in a lifetime" as well as "various trees and

tapeworms, where a single individual may produce thousands of litters" (p. 118). Thus,

126   Cole created, and contemporary theorists have inherited, a conception of parity as a

discrete variable: an organism either reproduces more than once or it doesn't.

128   Cole also identified "the paradox of semelparity", and wrote that "for an annual

species, the absolute gain in intrinsic population growth which could be achieved by

130   changing to the perennial reproductive habit would be exactly equivalent to adding one

individual to the average litter size" (Cole 1954, p. 118). Consequently, according to the

132   model he developed, a semelparous or iteroparous strategy evolves in response to strong

directional selection for trait-values that: (1) maximize the annual rate of intrinsic

134   increase; and (2) are subject to tradeoffs, since reproductive effort is always limited by

resource availability. The "paradox of semelparity" is that the relative intrinsic rates of

136   increase for semelparous and iteroparous strategies are very similar (i.e. they differ only

by one individual—the mother), which suggests that iteroparity, not semelparity, should

138   be rare, while in nature, iteroparous life histories are generally more common than

semelparous ones. Cole's articulation of the paradox of semelparity motivated many

140   studies searching for theoretical selective advantages of traits linked to discrete

semelparous and iteroparous strategies (Murdoch, 1966; Murphy, 1968; Omielan, 1991;

142   Su and Peterman, 2012; Vaupel et al., 2013; Cushing, 2015), as well as attempts to detect

these selective advantages in natural systems (Murphy and Rodhouse, 1999; Kaitala et

144   al., 2002; Kraaijeveld et al., 2003; Franklin and Hogarth, 2008; Gagnon and Platt, 2008;

Fisher and Blomberg, 2011). Following Cole, semelparous strategies considered in later

146   life history models were usually also annual (although empirical data on long-lived

semelparous organisms was also collected, e.g. Young and Augspurger, 1991; García,

148   2003), and thus the primary goal of many models purporting to explain the evolution of

semelparity was to provide reasons why a perennial-iteroparous strategy might confer

150   higher fitness than an annual-semelparous one.

Cole's "paradox of semelparity" was resolved by acknowledging that differences

152   in age-specific rates of mortality affect the relative fitness of semelparous and iteroparous

habits. Building on prior analytical work (see: Murphy, 1968; Emlen, 1970; Gadgil and

154   Bossert, 1970; Bryant, 1971), Charnov and Schaffer (1973) and Schaffer (1974b) noted

that the expected fitness value of individuals at juvenile (i.e. prereproductive) and adult

156   (i.e. reproductively mature) developmental stages often differed. They then argued that

when the survival of adults was more assured than the survival of juveniles, an

158   iteroparous habit would have a growth advantage over a semelparous one. Thus, their

model emphasized that the value of the age class with a lower age- or stage-specific rate

160   of mortality was—assuming equal fitness across age classes—greater than the value of

the age class with a higher rate of mortality. Young (1981) extended this insight into a

162   more general model of intrinsic rates of increase, which incorporated not only differences

in age-specific survivorship, but also differences in prereproductive development time

164   and time between reproductive episodes. This model provided three major reasons why

semelparity might be favoured by natural selection. First, high adult mortality—or the

166   early onset of reproductive senescence—might prevent iteroparous species from accruing

fitness gains from established parents over long timescales. Second, a high population

168   growth rate should favour semelparity outright. Third, when the marginal cost of

additional offspring is inversely proportional to the number of offspring produced,

170   fecundity is maximized by investing all reproductive effort into a single episode, i.e.

adopting an extreme annual-semelparous life history—see also Schaffer (1974) and

172   Schaffer and Gadgil (1975).

174   **(2) Further theoretical work on parity as a discrete trait**

Given that earlier work sought to explain the prevalence of semelparous and

176   iteroparous strategies by identifying differences in age-specific mortality, recent work has

sought to explain why differences in age-specific mortality persist, as well as how

178   varying environmental conditions facilitate the co-existence of different modes of parity.

Bulmer (1985, 1994) incorporated a model that incorporated density-dependence, a

180   model that was generalized by Ranta et al. (2002). Another common approach has been

to use simulations, based on comparisons between discrete strategies, to argue that spatial

182   heterogeneity and stochastic events (i.e. demographic disasters and windfalls) influence

the evolutionary stability of each mode of parity over small spatial scales (e.g. Ranta et

184   al., 2001). Similarly, Zeineddine and Jansen (2009) examined the role that discrete modes

of parity may play in evolutionary tracking, suggesting that species adopting an annual-

186   semelparous strategy may have an evolvability advantage over perennial-iteroparous

congeners. Moreover, considerable evidence now supports two general conclusions: (1)

188   that theoretically optimal life history strategies strongly depend on optimizing parity

(Maltby and Calow, 1986; Keeley and Bond, 1999; Iguchi and Tsukamoto, 2001;

190   Stegmann and Linsenmair, 2002; Kraaijeveld et al., 2003; Leiner et al., 2008; Trumbo,

2013), but also (2) that parity is especially important for predicting reproductive

192   scheduling (Schaffer and Gadgil, 1975; Kozłowski and Wiegert, 1986; Iwasa, 1991;

Kozłowski, 1992; McNamara, 1997; Cooke et al., 2004; Miller et al., 2012; Vaupel et al.,

194   2013; Oizumi, 2014), and/or the optimal allocation of reproductive effort to offspring

(Cohen, 1966; Smith and Fretwell, 1974; Winkler and M., 2002; Einum and Fleming,

196   2007; Gremer and Venable, 2014; Mironchenko and Kozłowski, 2014). Thus the current

theoretical life history literature is replete with papers discussing the knock-on effects of

198   the assumption that modes of parity are discrete rather than continuous.

200   **(3) Empirical support for the discrete conception of parity**

Empirical support for the discrete model of parity is strongest where perennial-

202   iteroparous and annual-semelparous (or, rarely, perennial-semelparous) congeneric

species have starkly different life histories. For instance, in a comparison of Mount

204   Kenya species of the genus *Lobelia*, Young (1984) found that juvenile and adult mortality

of the annual-semelparous species *L. telekii* were higher than in the closely related

206   perennial-iteroparous species *Lobelia keniensis*. Young concluded that the difference in

age-specific rates of mortality would strongly influence the expected value of future

208   reproduction for each species, leading to perennial-iteroparity in one species and annual-

semelparity in the other (Young, 1990). Similar comparisons between semelparous and

210   iteroparous congeners or confamilials have been conducted in insects (Fritz et al., 1982;

Stegmann and Linsenmair, 2002), salmon (Dickhoff, 1989; Unwin et al., 1999; Crespi

212   and Teo, 2002; Kindsvater et al., 2016), snakes (Bonnet, 2011), algae (De Wreede and

Klinger, 1988) and dasyurid marsupials (Kraaijeveld et al., 2003; Mills et al., 2012).

214   Other studies have focused on reproductive effort, since a declining marginal cost of

offspring in terms of reproductive effort should select for an annual- or perennial-

216   semelparous life history over an perennial-iteroparous one. This is the cited cause of the

evolution of semelparity in *Digitalis purpurea* (Sletvold, 2002), and in *Antechinus agilis*

218   (Smith and Charnov, 2001; Fisher and Blomberg, 2011). Growth rate is also important; in

two subspecies of *Yucca whipplei*, the semelparous variant showed higher viability and

220   faster time to germination than the iteroparous variant did (Huxman and Loik, 1997).

Further studies highlight the mortality differences between juveniles and adults, which

222   explains the evolution of semelparity in a variety of long-lived semelparous plants

(Foster, 1977; Kitajima and Augspurger, 1989; Young and Augspurger, 1991), as well as

224   in salmonids (Fleming, 1998; Crespi and Teo, 2002; Hendry et al., 2004; Sloat et al.,

2014).

226   Models have been developed that use demographic parameters to predict age and

size at first flowering for semelparous (monocarpic) plants; however, these models have

228   been found to be more appropriate for long-lived than short-lived species (Metcalf et al

2003, Rees and Rose 2002). More recently, mathematical modelling of evolutionary

230   responses to discrete semelparous and iteroparous strategies has focused on whether the

maintenance of both modes of parity can be a consequence of stochasticity in the ratio of

232   juvenile to adult mortality (Murphy, 1968; Ranta et al., 2002), of differences in the

effects of density on age-specific mortality (Bulmer, 1985), or as a consequence of

234   population instability (Ranta et al., 2000).

236   **III – The continuous conception of parity**

        (1) From uniparity to continuous reproduction

238   However, in many cases substantial unexplained variation in parity exists even

        after factors such as age-specific mortality, density dependence, and environmental

240   effects are taken into account. For this reason it seems as though models based on the

        discrete conception of parity describe a limited range of special cases and not the

242   majority of systems with congeneric or confamilial species with different reproductive

        strategies. This problem arises because theoretical models of the discrete conception of

244   parity make two characteristic assumptions. First, these models assume that reproductive

        output is allocated among cycles (typically seasons or years) rather than expressed

246   continuously. This means that offspring produced at two different times within a single

        season are "counted" as being part of the same reproductive episode, while offspring

248   produced at two different times in two different seasons are counted as part of

        categorically different reproductive episodes. This permits the calculation of threshold

250   values (e.g. of size or age) beyond which selection should begin to favour one mode of

        parity or the other, but is based on a distinction that is arbitrary. Second, each individual

252   is assumed to express a single reproductive strategy; models do not predict

        phenotypically plastic modes of parity, or facultative switching between modes.

254   These assumptions do not hold in many cases. The fact that semelparous

        reproduction rarely occurs "once"—i.e. in exactly one place, at exactly one time—has led

256   to a new treatment of parity as continuously varying between extremes of "pure"

        semelparous and iteroparous reproduction. This approach has gained traction because

258   there is considerable ambiguity in "breeding once" (Kirkendall and Stenseth, 1985).

Moreover, "annuality" and "perenniality"—terms that refer to the number of years in

260   which organisms reproduce—cannot be used interchangeably with "semelparity" and

"iteroparity", which refer to the number of reproductive episodes organisms have (Fritz et

262   al., 1982; Kirkendall and Stenseth, 1985). In "The Evolution of Life Histories", Roff

(1992) noted that, "if we consider our unit of time to be a single year, annuals can be

264   termed semelparous and perennials iteroparous. A further division is possible within

annuals, for some reproduce once and are, therefore, semelparous within any time scale,

266   while others flower repeatedly throughout the summer and, hence, are iteroparous with

respect to annuals that flower only once, but semelparous with respect to perennials" (p.

268   248). That is, it is the simultaneity and the finality of the reproductive episode (i.e. the

concentration of reproductive effort) that defines perfect semelparity. Therefore, the

270   continuous conception characterizes "extreme" semelparity to be a single, complete, and

exhaustive reproductive episode where all reproductive effort is invested at once.

272   Examples of this strategy—which Kirkendall and Stenseth (1985) termed "uniparity"—

include mayflies and mites of the genus Adactylidium (Edmunds et al., 1976; Corkum et

274   al., 1997). Both male and female mayflies die shortly after mating and dispersing

fertilized eggs. In Adactylid mites, offspring devour the mother from the inside out, and

276   are thus obligately annual-semelparous (Elbadry and Tawfik, 1966; Goldrazena et al.,

1997). The correspondingly "extreme" perennial-iteroparous strategy is a long-lived

278   perennial strategy that spreads reproductive effort out evenly among a very large number

of reproductive cycles. Many species, including bristlecone pine, many deep-sea

280   zoanthids, and other supercentennial species that reproduce regularly show such a habit

(Baker, 1992; Druffel et al., 1995; Finch, 1998; Rozas, 2003). Intermediate strategies

282   complete reproduction over a shorter timescale than bristlecone pine, but over a longer

timescale than Adactylid mites.

284   The continuous conception of parity is therefore very simple: parity is a trait like

any other, and continuous variation in factors affecting reproduction (e.g. resource

286   availability, timing of reproduction, etc.), where subject to evolution by natural selection,

should result in continuous variation in reproductive strategy (see: Salguero-Gómez et al.,

288   2016). Furthermore, rather than considering only whether organisms complete

reproduction within a given year, and making no finer distinction, life history strategies

290   should be compared by the degree to which they concentrate or disperse reproductive

effort—and hence risk of reproductive failure—in time. For example, a mature biennial

292   strategy (where an organism reproduces once per year in two consecutive years)

distributes reproductive effort over a shorter timescale than does a long-lived perennial

294   congener (where an organism reproduces once per year in many years); although the

biennial strategy is not semelparous, it is further toward the "uniparous" end of the

296   continuum of modes of parity than is the perennial strategy. Similarly, an annual-

semelparous life history that reproduces rapidly lies further toward this end of the

298   continuum than does an annual-semelparous life history in which reproduction is spread

over a longer period of time.

300

(2) Empirical support for the continuous conception of parity

302   There is considerable empirical support, from lab and field studies alike, for the notion that parity varies continuously. These results have made it increasingly clear that

304   demographic explanations rooted in the discrete model of parity fail to provide an universal evolutionary explanation for the appearance of different modes of parity. The

306   most obvious objections to the universal applicability of this theory come from species that are facultatively semelparous, from species that reproduce irregularly or

308   opportunistically, or from comparisons between related iteroparous and semelparous species that do not show measurable differences in factors affecting intrinsic rates of

310   increase, including age-specific rates of mortality. These situations are not uncommon in nature. The problem they present is significant because the evolutionary transition from

312   semelparity to iteroparity (and back) is ubiquitous, and has occurred in a wide variety of taxa (see Table 1 for an example using data from angiosperm orders).

314   There are important consequences for adopting the continuous conception of parity as a starting point for modelling the evolution of different modes of parity.

316   Mathematical models based on the discrete conception of parity often predict threshold values—in mortality rate, size at initiation of reproduction, or expected growth rate—that

318   do not agree with empirical observation (Omielan, 1991; Lessells, 2005; Piñol and Banzon, 2011; Su and Peterman, 2012; Trumbo, 2013; Vaupel et al., 2013). In particular,

320   ESS models derived from assumptions rooted in the discrete conception of parity frequently underestimate the adaptive value of semelparous reproductive strategies; even

322   after accounting for the effects of environmental stochasticity and density-dependence, ESS models predict that semelparous strategies should be less abundant—and less fit—

324   than they have been found to be (Benton and Grant, 1999). In addition, there are

empirical cases that explicitly do not conform to the predictions of the discrete model.

326 For example, an analysis of 12 winter-establishing primrose species (Oenothera:

Onagraceae) found no significant differences in mortality estimates or in environmental

328 determinants of fitness for semelparous and iteroparous species (Evans et al., 2005). In

some cases, the problem may be that life histories are too complex for organisms to

330 follow discrete strategies; many salmon species also do not fit neatly into "classical"

annual- or perennial-semelparous and perennial-iteroparous classifications (Unwin et al.,

332 1999; Hendry et al., 2004). Other research has suggested that deterministic models of

investment may better fit long-lived than short-lived semelparous species, given that

334 many annual semelparous species (usually plants) show substantial phenotypic plasticity

in phenology (e.g. size at first flowering), offspring quality and overall fecundity (Burd et

336 al., 2006).

In order to provide a coherent exposition of the extensive body of recent work that

338 shows empirical support for the continuous conception of parity, in what follows I focus

on three "intermediate" life histories that are neither annual-semelparous nor perennial-

340 iteroparous, but express another mode of parity that falls somewhere in between. These

include: (1) facultative iteroparity; (2) facultative semelparity; and (3) phenotypically

342 plastic parity. Although these three examples are the most common modes of parity that

are neither classically (annual- or perennial-) semelparous nor iteroparous, other

344 intermediate strategies exist, particularly when species or clades have idiosyncratic life

histories. In addition, an individual population or species may itself express multiple

346 modes of parity. For instance, arctic cod (*Boreogadus saida*) are annual-semelparous in

nature, but can reproduce in two consecutive years in captivity, making them

348   facultatively iteroparous (Hop et al., 1995; Hop and Gjosaeter, 2013). However, males

and females of this species also seem to have different life histories – males begin to

350   reproduce at an earlier age, and can allocate extreme amounts of reproductive effort to a

single instance of reproductive activity; semelparity in this species is thus also

352   phenotypically plastic (Nahrgang et al., 2014). Although examples of each life history are

provided below, many more have been added to Table 2, a list of species showing

354   facultatively varying or plastic modes of parity.

356   *(a) Facultative Iteroparity*

Many semelparous species have shown the ability to facultatively reproduce one

358   or more times after an initial bout of reproduction has began and ended—this is termed

"facultative iteroparity". Facultative iteroparity can be adaptive when it either: (1)

360   provides an opportunity to realize fitness gains from an unexpected abundance of

resources, or (2) shifts reproductive effort from inopportune to opportune times. The first

362   type of adaptive facultative iteroparity occurs when additional bouts of reproduction

increase fitness by permitting unexpected "bonus" resources to be invested in new

364   offspring. For example, mothers of the semelparous crab spider *Misumena vatia* (Araeae,

Thomsidae) typically lay and provision a single brood of eggs (Gertsch, 1939; Morse,

366   1979), however in response to high food availability and/or usually warm environmental

conditions, they are capable of laying and caring for a second brood if sperm supplies are

368   not depleted (Morse, 1994). A similar facultative double-broodedness in response to

unusually favourable environment has been observed in the green lynx spider *Peucetia*

370   *viridans* (Fink, 1986). In addition, a small proportion of Chinook salmon

(*Onchorhynchus tshawytscha*), which typically reproduce only once, have been found to

372   survive and reproduce in two or three additional seasons (Unwin et al., 1999). Tallamy

and Brown (1999) showed that large, well-provisioned female burying beetles in multiple

374   species in the genus Nicrophorus can reproduce more than once, despite the fact that

small females can typically breed only once.

376   The second form of adaptive facultative iteroparity occurs when deferral of

reproductive effort—from a primary reproductive episode to a secondary one—allows an

378   organism to reproduce at a more opportune time. Reproduction is deferred to seek the

highest marginal fitness return on invested reproductive effort. For example, when high

380   organic pollution levels disrupt primary reproduction in the freshwater leech *Erpobdella*

octoculata, reproduction ceases and remaining reproductive effort is deferred to a second

382   reproductive bout produced the next year (Maltby and Calow, 1986). Similar behaviour

has been seen in another Erpobdellid leech, *Erpobdella obscura* (Peterson, 1983; Davies

384   and Dratnal, 1996) as well as in many cephalopods (Rocha et al., 2001). Adaptive

deferral of reproductive effort is common in crab spiders. In *Lysiteles coronatus*, artificial

386   brood reductions resulted in the production of a second brood, and the degree of deferral

was proportional to the degree of the original reduction (Futami and Akimoto, 2005).

388   This was also observed in the field in Eresid spiders of the genera Anelosimus and

Stegodyphus, both of which facultatively produce a second brood in response to nest

390   predation (Schneider and Lubin, 1997; Schneider et al., 2003; Grinsted et al., 2014).

Although the adaptive potential of facultative iteroparity is often apparent, facultative

392   iteroparity may also be vestigial instead of adaptive. In this case, the organism's life

history merely reflects an ancestral state, and the second (or additional) bout of

394   reproduction should confer little or no adaptive value (Golding and Yuwono, 1994;

Hughes and Simons, 2014b).

396

(b) Facultative Semelparity

398   Facultative semelparity occurs when species that are normally perennial-

iteroparous—i.e. have multiple, discontinuous reproductive episodes that span more than

400   one year—are capable of expressing only a single reproductive bout (Christiansen et al.,

2008). This is a useful strategy for organisms to use to take advantage of unusually good

402   environmental conditions for reproduction. For example, in the short-lived mustard

Boechera fecunda (also known as *Arabis fecunda*; Brassicaeae), plants are capable of

404   wide range of reproductive strategies, from near-instantaneous semelparity to multi-year

iteroparity. This is because *B. fecunda* can produce many small axillary inflorescences in

406   any given year, and their production does not preclude flowering by the same rosette in

the subsequent year. However, plants can also produce large "terminal inflorescences"

408   that exhaust remaining resources and lead to senescence and death. Although some plants

produce axillary inflorescences for several years before a terminal inflorescence, others

410   produce a terminal inflorescence in their first year (Lesica and Shelly, 1995; Lesica and

Young, 2005). A similar system is seen in common foxglove, *Digitalis purpurea*

412   (Scrophulariaceae), which is predominantly biennial or perennial-iteroparous, but can be

facultatively semelparous if resource availability in the first year is high (Sletvold, 2002).

414   Facultative semelparity has also been observed in capelin (Christiansen et al., 2008; Loïc

416   et al., 2012), squid, soil microarthropods (Siepel, 1994), dasyurid marsupials (Kraaijeveld et al., 2003; Martins et al., 2006), and in the flowering plants *Ipomopsis aggregata* (Silvertown and Gordon, 1989) and *Cynoglossum officinale* (Williams, 2009). Some

418   facultatively semelparous species show a continuous range of types of reproductive episode, rather than discretely fatal or non-fatal ones. *Erysimum capitatum* (Brassicaceae)

420   produces multiple reproductive episodes in environments where water is plentiful; however, where water is scarce it expresses a semelparous strategy (Kim and Donohue,

422   2011).

(c) Phenotypically Plastic Parity

424   Like other traits, mode of parity can be phenotypically plastic. This occurs when different modes of parity are expressed by a single species in response to environmental

426   cues. Different modes of parity can occur both: (1) among individuals; or (2) within the reproductive episode of a single individual. Phenotypically plastic mode of parity is

428   common source of intraspecific variation in life history characters; thus this is a major source of confusion for mathematical models that predict a single optimal value for all

430   semelparous and all iteroparous habits. Such differences need not be dramatic—for example, as a consistent response to environmental triggers, even small differences in the

432   length of a semelparous reproductive episode may have significant effects on fitness.

        Strong empirical evidence of phenotypically plastic mode of parity is found in sea

434   beets (Beta spp., Amaranthaceae), which display reproductive strategies along "a gradient from pronounced iteroparity to pronounced semelparity" (Hautekèete et al., 2001, p.

436   796). Interestingly, the selective pressures faced by these species seem to elicit similar

plastic responses. Environmental stressors cause individuals to trade off future fecundity

438   for increased immediate reproductive effort, resulting in a parity gradient tending to

semelparity when environmental stress becomes intense (Hautekèete et al., 2001, 2009).

440   This pattern is consistent with the prediction that higher current reproductive effort can

prevent organisms from being exposed to uncertain or risky environments (Williams,

442   1966; Vahl, 1981; Rubenstein, 2011; Trumbo, 2013). Similar trade-offs were observed in

Yucca whipplei (Huxman and Loik, 1997), *Chusquea ramosissima* (Montti et al., 2011),

444   and *Onopordum illyricum* (Rees et al., 1999). *Lobelia inflata* is capable of producing

different semelparous strategies, from a nearly instantaneous annual-semelparity, where

446   plants produce many similar flowers quickly and simultaneously, to (nonadaptive)

facultative biennial-iteroparity, where as much as half of all reproductive effort is

448   invested in a second reproductive episode. The time of initiation of reproduction strongly

predicted which of these strategies is realized (Hughes and Simons, 2014b; c).

450   Many insect species are also capable of displaying a range of modes of parity

among individuals (Trumbo, 2013). In the assassin bug (*Atopozelus pallens*), females

452   deposit eggs in small clutches, approximately every two days. However, the number of

clutches—and hence how prolonged this reproductive episode is—varies substantially

454   (Tallamy et al., 2004). Similarly, European earwigs (*Forficula auricularia*) show

condition-dependent semelparity; females either deposit all eggs into a single clutch or

456   lay two clutches (Meunier et al., 2012; Ratz et al., 2016). Most insects showing variation

in the number of clutches produced do so in response to abiotic cues, particularly

458   temperature and day length (Bradshaw, 1986). This behavior can also be found in

ascidarians (Grosberg, 1988) and semelparous mammals (Wolfe et al., 2004; Mills et al.,

460   2012).

Phenotypic plasticity within a reproductive episode of a single individual is

462   noticeable when a semelparous organism displays a changing reproductive strategy—

varying along the continuum of parity—that cannot be attributed to developmental,

464   environmental, or architectural constraints (Diggle, 1995, 1997). This pattern is more

difficult to detect than phenotypically plastic strategies that differ between individuals,

466   but in many systems observable differences exist between the "packaging" of

reproductive effort, resulting in adaptive variation in phenology or offspring quality

468   through time. This can be difficult, since because they reproduce only once, semelparous

organisms are expected to show high reproductive effort (Bonser and Aarssen, 2006).

470   However, the development of fruits of the semelparous plant *Lobelia inflata* varied

continuously; in this system, late fruits showed accelerated phenology and higher

472   offspring quality relative to early fruits. This pattern, which indicated that more

reproductive effort was invested in later fruit, shows that *L. inflata* does not "reproduce

474   once" but dynamically allocates reproductive effort throughout a sequence of repeated

fruiting events ((Hughes and Simons, 2014a, 2015). Likewise, in populations of the

476   semelparous plant *Centaurea corymbosa*, plants showed highly variable life cycles—

dynamically varying the proportion of reproductive effort allocated to sequential

478   flowers—depending on environmental conditions and crowding (Acker et al., 2014).

480   **(3) Evolutionary transitions between modes of parity are ubiquitous**

Transitions between different strategies along the semelparity-iteroparity

482 continuum are common throughout the tree of life. Furthermore, modes of parity appear

to be evolutionarily labile within species, and many species show significant intraspecific

484 differences in the expression of parity (e.g. Maltby and Calow, 1986; Hughes and

Simons, 2014a; c). Thus while some clades consistently display a single mode of parity

486 (e.g. most placental mammals are exclusively iteroparous), many clades show

considerable variability (see Table 1 for data from plant orders). Among cephalopoda

488 (Mollusca), *Loligo opalescens*, *Octopus vulgaris*, *O. mimus*, and *O. cyanea* display

extreme semelparity (Ikeda et al., 1993; Rocha et al., 2001), while *Nautilus* spp. show

490 extreme perennial-iteroparity (Ward, 1983, 1987). However, other cephalopods,

including *Octopus chierchiae*, *Sthenoteuthis oualaniensis*, and *Dosidicus gigas* show

492 varying degrees of facultative iteroparity (Nesis, 1996; Laptikhovsky, 1998, 1999; Rocha

et al., 2001), while still others, including *Sepia officinalis*, *Loligo vulgaris*, *L. bleekeri*, *L.*

494 *forbesi*, and *Ilex coindetii* show facultative semelparity, and, in the case of *S. officinalis*, a

strikingly variable duration of reproduction (Boletzky, 1987, 1988; Baeg et al., 1993;

496 Gonzalez, 1994; Gonzalez and Guerra, 1996; Rocha and Guerra, 1996; Melo and Sauer,

1999). Furthermore, in many of these species key traits—such as the timing and duration

498 of reproduction—show substantial dependence on environmental effects (Rocha et al.,

2001). Similar lability in these traits is also present in other clades, including both

500 angiosperms and animals (see: Maltby and Calow, 1986; Tallamy and Brown, 1999;

Hautekèete et al., 2001; Crespi and Teo, 2002; Varela-Lasheras and Van Dooren, 2014).

502 Thus, because evolutionary change from one mode of parity to another is a ubiquitous

life-history transition, accurately characterizing parity as a life-history variable of interest

504 may prove crucial to accounting for the adaptiveness of life-history strategies.

IV. UNDERSTANDING THE EVOLUTION OF PARITY AS A CONTINUOUS TRAIT

508   What changes should be made in light of the evidence that parity is a continuous

trait? In this section I will focus on three main recommendations. First, I provide a short

510 discussion of how seasonality should not be conflated with mode of parity. Second, I

discuss the necessity of developing new mathematical modelling approaches that treat

512 parity as a continuous variable. This is not simple, since parity itself is a composite trait,

and relies on the coordination of many biological functions at once. Third, I discuss why

514 ecologists should ground future studies of adaptive life history strategies in mechanistic

details derived from genetic studies of continuously-varying life history traits underlying

516 reproduction and, consequently, parity. These recommendations should improve both the

validity and reliability of predictive models of life-history evolution, while

518 simultaneously providing a framework for interpreting empirical findings regarding the

expression of reproductive effort through time.

520

(1) – Seasonality and Mode of Parity

522   One major implication of treating parity as a continuous variable is that this

reconception allows us to distinguish between parity and seasonality. Parity describes the

524   concentration or diffusion of reproductive effort in time, which is distinct from the

question of seasonal reproduction—i.e. how organisms should distribute reproductive

526   effort among seasons, when seasonal cycles determine the favourability of establishment,

growth, and reproductive conditions (Cole, 1954; Charnov and Schaffer, 1973; Schaffer,

528   1974b; Schaffer and Gadgil, 1975; Calow, 1979; Young, 1981; Bulmer, 1994; Evans et

al., 2005; Ranta et al., 2007). It is, of course, clear that seasonality is related to parity.

530   Insofar as an annual-semelparous organism is defined by the fact that it has a single

reproductive episode that occurs within one year, it is likely to experience selection for

532   strategies that optimize its reproductive schedule relative to season-specific

environmental effects; this means that an annual-semelparous organism is more likely to

534   show predictable seasonal patterns than a perennial-iteroparous congener that can escape

a poor season by overwintering. However, the explanatory power of such seasonal

536   adaptations may be much weaker when we compare a fast-reproducing semelparous

organism with a slower-reproducing semelparous congener, or when we compare an

538   iteroparous strategy where reproductive effort is distributed over two seasons with

another where reproductive effort is distributed among ten seasons. Seasonal effects are

540   likely to supervene on reproduction whenever regular intervals occur that have an impact

on the favourability of reproduction. Thus it may be more fruitful to understand annuality

542   and perenniality as strategies defined by the "digitization" of reproduction in response to

seasonality. The advantage of this approach is that it makes it easier to understand

544   flexible life histories, regardless of whether a species is semelparous or iteroparous.

There is widespread empirical evidence that seasonality and parity can vary

546   independently. One common pattern is integer changes in voltinism among organisms

that share a common mode of parity. For example, the Muga silkworm (*Antheraea*

548   *assamensis*) is semelparous and multivoltine throughout its natural range (from India to

Borneo). This species produces up to 6 generations per year, with the number of

550   reproductive cycles depending on length of the season (Singh and Singh, 1998; Ghorai et

al., 2009). However, the closely related Chinese tussar silkmoth, *Antheraea pernyi*, is

552   bivoltine at the southern margins of its range, but is univoltine in northern China and

Korea. Moreover, this continuous variation in voltinism along an ecological cline is due

554   to continuous variation in environment-dependent biogenic monoamine production in the

brains of diapause pupae (Fukuda, 1953; Matsumoto and Takeda, 2002; Liu et al., 2010).

556   Life histories also vary continuously among populations of the wild silkmoth (*Bombyx*

mandarina) and its domesticated counterpart (*Bombyx mori*), where populations in colder

558   climates (e.g. European Russia) are univoltine, whereas those in China and Korea are

bivoltine or multivoltine (Xia et al., 2009). Similar examples can also be found in

560   crucifers (Williams and Hill, 1986; Springthorpe and Penfield, 2015), orchids (Chase et

al., 2005), freshwater molluscs (Mackie and Flippance, 1983; McMahon and Bogan,

562   2001), and Centaurea (Asteraceae; Acker et al., 2014), among others. In each of these

systems, a distinct continuum of reproductive strategies despite the supervening effect of

564   seasonality is readily observable. Additionally, new models are being developed that

consider generation length independently from parity (Waples, 2016). Thus we can easily

566   tease apart the question of whether reproduction is concentrated in time—i.e. whether a

given species is semelparous—from the question of whether seasonality requires that, in

568   temperate climates, late-reproducing individuals should enter diapause rather than

reproduce immediately.

570

(2) Mathematical Models of Parity

572   A second problem facing life history theory is the challenge of making new

mathematical models that account for the continuity of modes of parity. Although

574   empirical studies of many taxa support the continuous conception of parity, the evolution

of different modes of parity from one another has generally been explained by

576   demographic models that compare the special case where annual-semelparous and

perennial-iteroparous strategies have different demographic implications. This means that

578   mathematical models that incorporate the assumption that there is a discrete difference

between semelparous and iteroparous strategies may not be able to account for the real

580   eco-evolutionary dynamics of the reproductive behaviour of many organisms that do not

show either annual-semelparous or perennial-iteroparous modes of parity, or the

582   reproductive behaviours of species or populations that display continuous differences in

parity. To develop a general model that can account for all modes of parity as adaptive

584   responses to environmental conditions should, as an axiom, treat parity as a continuous

trait, and should be able to explain both the evolution of semelparous strategies from

586   iteroparous ones (or vice versa) as well as the adaptive value of intermediate modes of

parity. In this section I argue that dynamic mathematical models that integrate molecular

588   data with demographic factors are the best candidates to explain the evolution of different

modes of parity. In addition, extant mathematical models used to explain the adaptive

590   differences between semelparous and iteroparous life histories—or to calculate "optimal"

trait values for distinct semelparous-annual and iteroparous-perennial strategies—can and

592   should be redesigned to incorporate a continuum of possible modes of parity.

These new models will have to build on and learn from a considerable body of

594   existing models detailing the eco-evolutionary dynamics of semelparous and iteroparous

life history strategies. Early conceptual and mathematical models of optimal semelparous

596   reproduction were generally simple, deterministic, and were designed to predict a single

"threshold" value that optimized life history characters such as size at first reproduction

598   (Bell, 1980; Young, 1981). Threshold models of this type include senescence-threshold

models based on the Penna aging model (Piñol and Banzon, 2011), as well as

600   development-threshold models such as age-structured life history models. Age-structured

models treat age at reproduction, and hence parity, as a discrete variable, and assess the

602   evolutionary consequences of the degree of overlap between juvenile (i.e.

prereproductive) and adult (reproductive) classes in a population (Wikan, 2012). Among

604   the best known of these are Leslie models, which predict either few evolutionary stable

states for semelparous organisms (Cushing, 2009, 2015; Cushing and Henson, 2012;

606   Cushing and Stump, 2013) or even that populations should consist entirely of individuals

of a given age class (Rudnicki and Wieczorek, 2014). Still other threshold models make

608   similar predictions for survival traits (Da-Silva et al., 2008).

However, despite rare exceptions (e.g. Lesica and Young, 2005), threshold

610   models generally fail to adequately predict reproductive phenotypes in field systems,

prompting some authors to emphasize the importance of making fewer assumptions that

612   contradict "real" life-history parameters—e.g. Burd et al. (2006) note that "empirical

attention to norms of reaction across growth environments will be a more profitable

614 approach than investigation of size thresholds per se". That is, for short-lived

semelparous species (and some long-lived semelparous species: see Rose et al., 2002),

616 the impact of stochastic variation is substantial, and of equal or greater importance than

the global optimum predicted by deterministic models (Rees et al., 1999). Furthermore,

618 Rees et al. (1999) show that that deterministic age-structured models, which rest on the

assumption that parity is discrete, consistently overestimate time at first reproduction in

620 monocarpic plants. Empirical evidence showing a wide and highly variable range of

reproductive phenotypes in natural populations (e.g. Marshall and Keough, 2007) has

622 prompted the formulation of new modelling approaches that consider a range of

semelparous strategies in response to environmental heterogeneity as a source of

624 stochasticity that confounds threshold models that consider semelparous reproduction to

be optimized for a given environmental (reviewed in Metcalf et al., 2003).

626   Recent mathematical models also fall into several types, each with a particular

ecological focus. Integral projection models, which incorporate random fluctuations in

628 environmental parameters related to reproduction, were developed to more accurately

predict time to first reproduction and size at reproduction, both in iteroparous species

630 (e.g. Kuss et al., 2008) and in semelparous species with a prolonged semelparous

reproductive episode (e.g. Rees et al., 1999; Ellner and Rees, 2006 Rees et al. 1999;

632 Sletvold 2005). Time-lagged models integral projection models attempt to account for the

temporal discounting of reproductive value as well as size-specific effects on

634 reproductive effort (Kuss et al., 2008). Newer age-structured stochastic models

incorporate continuous variation in life history traits to predict optimal timing of

636 reproduction; while these resemble earlier models that treat parity wholly as a discrete

638   variable, the life-history traits in these models are treated continuously (Oizumi and

Takada, 2013; Oizumi, 2014; Davison and Satterthwaite, 2016).

Several recent models have been developed to predict reproductive trait values

640   given other (measured or measurable) life history parameters. This modelling

methodology is intuitive and compatible with the idea that parity is a continuous trait. For

642   example, Kindsvater et al (2016) used a stage-structured model to assess the degree to

which trait covariation constrained life history adaptation in salmonids. Other kinds of

644   data-driven models fall into two main types: (1) models that highlight the importance of

phenotypically plastic reaction norms as maximizing fitness despite stochastic variability

646   in environment (e.g. Burd et al., 2006); and (2) models that emphasize the innate

variability in reproductive characters within species (e.g. Drouineau et al., 2014; Austen

648   et al., 2015). Both of these ideas may be useful in modelling selective pressures on a

continuum of modes of parity. Moreover, rather than using a single model to characterize

650   semelparous investment in flowers and offspring, authors are now proposing a 'meta-

modelling' approach to annual plant reproduction, recognizing that semelparous

652   reproduction can be fine-tuned by natural selection through phenotypic plasticity (Hughes

and Simons, 2014a). However, despite the success of some of these new models, as yet

654   they still suffer from a relative paucity of data relative to other areas of life-history

theory. When discussing models designed to predict the optimal timing of the initiation of

656   reproduction, Metcalf et al. (2003) wrote that, "a glaring inconsistency between the [life

history] models and the data is that all models predict a specific threshold flowering

658   condition…but data from natural population show a graded response".

One class of model that may prove to be useful in modelling the allocation of

660   reproductive effort over time are dynamic state variable models (DSVMs). DSVMs are

powerful dynamic optimization models used to characterize mechanistic relationships in

662   ecology, and have the benefit of being able to be solved computationally (Clark and

Mangel, 2000). Developing a DSVM can offer insight into the relative impact of

664   underlying causal processes (in this case, the underlying patterns of genetic regulation of

reproductive traits) on a state variable of interest (in this case, total plant fitness). Because

666   the model follows the value of a state variable, the effects of multiple fitness components

can be considered at once. Moreover, by parameterizing a DVSM with phenotypic data,

668   ecologists can determine the additive and multiplicative contributions of variation at

different gene loci, or between related phenotypes of interest. This is an important

670   advantage insofar as continuous models of parity should, where possible include

mechanistic detail. DSVMs are compatible with this approach: they can integrate a wide

672   range of functional, spatial, structural, behavioural, or environmental limitations

constraining investment in reproduction, and can generate testable predictions by

674   determining optimal reproductive decision schedules (e.g. Yerkes and Koops, 1999;

Skubic et al., 2004; Peterson and Roitberg, 2010).

676

(3) - Molecular Regulation of Parity

678   The third implication of understanding parity as a continuously varying trait is

that further study of parity should be rooted in mechanistic detail, and identifying the

680   mechanistic basis of different modes of parity (e.g. the contributions of individual genes

682 and/or molecular pathways responsible for initiating and continuing reproduction) should be an important priority for evolutionary ecology. Integrating theoretical ecology with molecular biological data was not possible when early life-history models were

684 developed, but since parity is determined by the onset and completion of reproductive episodes, and recent advances in molecular ecology have made it possible to understand

686 the physiological and genetic basis of these events in many systems, this is, in many systems, an achievable goal. Numerous examples of continuously-expressed

688 physiological processes result in continuous patterns of reproduction, and hence support the continuous conception of parity (Table 3). In this section, I will explain how parsing

690 out the contributions of a single gene can improve our understanding of how modes of parity can vary continuously. To do so, I will discuss an important example: the control

692 of the initiation of flowering in response to vernalization as it is regulated by FLOWERING LOCUS C (*FLC*) and its orthologues in the Brassicaceae. I discuss two

694 such cases: (1) FLC regulation of vernalization response in *Arabidopsis thaliana*, a semelparous annual; and (2) PEP1 regulation of vernalization response in *Arabis alpina*,

696 an iteroparous perennial.

In *Arabidopsis*, continuous variation in parity –i.e. the timing of floral initiation

698 and the duration of flowering—is determined by continuous expression of flowering-time genes, including *FLOWERING LOCUS T* (*FT*) (Kardailsky, 1999; Yanovsky and Kay,

700 2002; Kotake et al., 2003; Imaizumi and Kay, 2006; Turck et al., 2008; Simon et al., 2015), *FRIGIDA* (*FRI*) (Johanson et al., 2000; Le Corre et al., 2002; Michaels et al.,

702 2004; Stinchcombe et al., 2004; Shindo et al., 2005; Schläppi, 2006), *FLOWERING LOCUS C* (Coupland, 1995; Amasino, 1996; Michaels and Amasino, 1999; Sheldon et

704   al., 2000; Michaels et al., 2003, 2004; Bastow et al., 2004; Imaizumi and Kay, 2006; Kim

et al., 2007; Chiang et al., 2009), *GIGANTEA* (*GI*) (Fowler et al., 1999; Mizoguchi et al.,

706   2005; Jung et al., 2007), and *CONSTANS* (*CO*) (Redei, 1962; Putterill et al., 1995;

Koornneef et al., 1998; Samach et al., 2000; Suárez-López et al., 2001; Valverde et al.,

708   2004). Through different pathways, *GI* and *CO* activate the floral integrator gene

FLOWERING LOCUS T (*FT*), which transcribes a protein that activates floral identity

710   genes in the shoot apical meristem (Turck et al., 2008; Tiwari et al., 2010). In contrast,

FLC—along with *FRI*, which regulates *FLC* transcription—represses flowering in the

712   absence of vernalization.

Although much is known about the complex question of how flowering is

714   induced, here I concentrate on *FLC*, since continuous differences in *FLC* expression

cause continuous variation in the duration and timing of semelparous reproduction

716   (Wilzcek et al., 2009; Burghardt et al., 2015). This variation causes continuous

differences in parity. For instance, throughout Europe, parity in wild populations of

718   *Arabidopsis* seems strongly determined by climate and/or latitude: toward the colder

margins of its range, in northern Finland, plants show a fast-cycling summer semelparous

720   annual life history, while populations near the Mediterranean show a winter annual life

history, and populations in intermediate locations (e.g. the UK) display intermediate life

722   histories (Thompson, 1994; Méndez-Vigo et al., 2011; Ågren and Schemske, 2012). Lab

studies have identified *FLC* as the mechanism responsible for this life-history variation.

724   For example, Wilzcek et al. (2009) introgressed a functional *FRI* allele into *A. thaliana*

ecotypes with nonfunctional alleles. They predicted that this genetic modification—

726   which causes the upregulation of *FLC*—would see plants transition from a summer-

annual to winter-annual life history. Instead, plants with functional *FRI* alleles flowered

728   only 10 days later than those with nonfunctional *FRI* alleles, causing the authors to note

that their results "suggest that *A. thaliana* ecotypes cannot simply be divided into two

730   discrete classes of winter-annual and rapid-cycling genotypes. Rather, most ecotypes may

be capable of both life histories" (p. 933). This prediction is consistent with recent data

732   from studies of the impact of *FLC* on the life histories of *A. thaliana* ecotypes sourced

from different parts of its native range. While populations varying at the *FLC* locus show

734   substantial local adaptation with respect to important life history traits—including those,

such as length of duration of reproduction, which underlie mode of parity—most

736   ecotypes adopt new life histories when translocated to radically different environments

(Ågren and Schemske, 2012; Dittmar et al., 2014; Ågren et al., 2016; Postma and Ågren,

738   2016).

Where the prevalence of different *FLC* alleles differs between populations,

740   differential expression of FLC can result in different flowering phenologies, and even

different modes of parity (Johanson et al., 2000; Michaels et al., 2004; Schläppi, 2006;

742   Banta and Purugganan, 2011). This is likely an adaptive response; life-history models of

the natural genetic variation at the *FLC* and *FRI* loci have shown that *FLC* expression

744   explains a relatively high level of variation in fitness (Donohue et al., 2014; Burghardt et

al., 2015; Springthorpe and Penfield, 2015). Moreover, empirical studies suggest that

746   such fitness differences may account for the latitudinal cline in *Arabidopsis* life history

found in natural populations (Caicedo et al., 2004). Thus it seems that local adaptation of

748   different modes of parity result from populations experiencing stabilizing selection for

climate-appropriate *FLC* alleles (Postma and Ågren, 2016).

750   While fitness differences are tightly linked to phenotypic variation, major plant

phenotypes such as flowering phenology are highly plastic in *Arabidopsis*. The genetic

752   and epigenetic regulation of *FLC* regulate the timing of important life-history transitions,

determining a plant's reproductive schedule, and hence its mode of parity (Albani and

754   Coupland, 2010; Turck and Coupland, 2014). However, environmental factors such as

seed maturation and germination temperatures can interact with plant genotypes to

756   produce "clusters" of phenotypically similar, yet genotypically distinct, plant phenologies

(Burghardt et al., 2016). Environmental variation can therefore facilitate the adoption of

758   multiple flowering phenologies (e.g. summer annual, winter annual, rapid cycling, etc.)—

and thus modes of parity—from a single *Arabidopsis* ecotype (Simpson and Dean, 2002;

760   Méndez-Vigo et al., 2011).

        The relationship between *FLC* and variation in mode of parity is best understood

762   in *Arabidopsis*, continuous variation in parity arising from response to vernalization has

also been identified in the confamilial species *Arabis alpina*. *PERPETUAL FLOWERING*

764   *1* (*PEP1*), the orthologue of *FLC* in *A. alpina* (Wang, Farrona, Vincent, Joecker, et al.,

2009), is responsible for regulating vernalization response. In *Arabidopsis*, *FLC* confers a

766   obligate vernalization requirement on individuals; thus flowering is not possible until

plants experience winter temperatures, which causes chromatin remodeling that prevents

768   *FLC* transcription (Sheldon et al., 2000; Bastow et al., 2004). *PEP1* also confers an

obligate vernalization requirement to *A. alpina*, however this effect is (seasonally)

770   temperature-dependent. That is, in the Pajares ecotype, *PEP1* transcription is temporarily

repressed by low temperatures, mediated by the continuous expression of *COOLAIR*-

772   family antisense RNAs produced in response to cold (Wang, Farrona, Vincent, Joecker,

et al., 2009; Albani et al., 2012; Castaings et al., 2014a), and thus facilitating the regular

774   alternation of vegetative and reproductive phases that characterize iteroparous-perennial

life histories. Like *FLC*, considerable natural variation exists at the *PEP1* locus—most

776   natural *A. alpina* ecotypes have a functional *PEP1* allele, and under controlled conditions

restrict flowering duration, although some accessions lack a functional *PEP1* allele, and

778   thus continuously flower without vernalization (Torang et al., 2015). That *PEP1* alone is

responsible for this phenotype has been confirmed using mutant lines (Wang, Farrona,

780   Vincent, Joecker, et al., 2009; Wang et al., 2011; Albani et al., 2012; Bergonzi et al.,

2013). However, this transition is continuous rather than discrete, since the degree of

782   *PEP1* suppression depends both on *PEP1* allele present in the accession as well as the

duration of vernalization.

784   Thus, in both *Arabidopsis thaliana* and *Arabis alpina* (among other Brassicaceae

spp.), parity is linked to genetic variation at the FLC/PEP1 locus, and alleles from

786   different, locally-adapted ecotypes show a range of distinct phenotypes (Aikawa et al.,

2010; Kemi et al., 2013; Zhou et al., 2013). Moreover, FLC itself is subject to a number

788   of regulatory mechanisms, some of which result in independent life history differences

(Gazzani et al., 2003; Shindo et al., 2005, 2006). *FLC* example is not an isolated case, nor

790   have genes linked closely to parity been discovered only in plant species; although a

comprehensive description of all genes linked to parity in all species is beyond the scope

792   of this article, a few notable examples from a variety of well-studied taxa are presented in

Table 3. Genes linked to traits underlying parity, including reproductive maturation,

794   stress response, reproductive phenology, and senescence, have been the subject of many

informative reviews (see: McBlain et al., 1987; Finch and Rose, 1995; Tower, 1996;

796   Danon et al., 2000; Eulgem et al., 2000; Rion and Kawecki, 2007; Garcia De Leaniz et

al., 2007; Hall et al., 2007; Schneider and Wolf, 2008; Xin et al., 2008; Costantini et al.,

798   2008; Amasino, 2009; Thomas et al., 2009; Partridge, 2010; McCormick et al., 2011;

Selman and Withers, 2011; Kenyon, 2011; Thomas, 2013; Blümel et al., 2015; Wang et

800   al., 2015).

V. CONCLUSIONS

802

We still know far too little about why the evolutionary transition from semelparity

804   to iteroparity (or vice versa) is as common as it is, or under which ecological conditions

intermediate strategies—such as facultative semelparity—will thrive. While models

806   rooted in the conception of parity as a binary trait do a good job of accounting for the

fitness differences between discrete semelparous-annual and iteroparous perennial

808   alternative strategies, systems characterized by only these possibilities—and no others—

are special cases. In many cases the life history question at hand is more subtle: why does

810   a given species evolve a facultative strategy, or why does another show intraspecific

variation in the length of the semelparous reproductive episode? In such cases—which

812   are not as rare as they were when the adaptiveness of parity was first being investigated—

the discrete conception of parity is a impractical oversimplification.

814   Thus the main conclusion of this work is that parity should be treated as a

continuous trait rather than a discrete one. This reconception of parity offers several

816   notable advantages for life-history theory. First, treating parity as a continuous trait

allows us to treat parity as a distinct life history syndrome, itself the result of correlated

818   selection on a suite of traits, that may show finely-graded correlated variation within

species or populations. This is advantageous because parity is a composite trait, and the

820   act of reproducing at a given time, of a given duration, etc. involves the recruitment and

coordination of many independent parts, each of which may affect the expression of

822   others. An integrative approach has proven to be valuable in studying other multifactorial

composite traits (e.g. Buoro and Carlson, 2014). Furthermore, whether they share

824   common genetic basis or not, obvious or visible life history characters may not be

primary targets of selection, and evolution of such traits may occur as an epiphenomenon

826   of selection on (one or many) other apparent or non-apparent underlying traits. Second,

developing accurate mathematical and mechanistic models designed to explain fitness

828   differences between life histories—as well as to understand the nature of the costs and

trade-offs associated with initiating and completing reproductive episodes—will be best

830   understood by acknowledging that living systems show a continuum of reproductive

strategies between annual-semelparity and perennial-iteroparity. Considering only

832   annual-semelparity and perennial-iteroparity as discrete alternatives, although a useful

simplification for many models, is biologically accurate only in a limited number of

834   special cases, and the continuous conception of parity is more likely to approximate the

eco-evolutionary dynamics of natural systems that show intraspecific or plastic variation

836   in the expression of parity. Finally, treating parity as a continuous variable that represents

a syndrome of associated traits may make it easier to integrate life history studies with

838   mechanistic details deriving from molecular ecology, insofar as composite life history

traits such as parity are unlikely to be the result of a simple presence or absence of a

840   single gene or allele. Instead, parity is likely to be the product of complex systems of

genetic, translational, and post-translational regulation.

842

There are important issues to consider for further work on a continuum of modes

844   of parity. First, life-history theorists should make their language clearer and tighten

definitions, in order to avoid confusion and improve the effectiveness of evolutionary

846   explanations. Parity, the degree of temporal concentration or diffusion of reproductive

effort in time, is a distinct evolutionary question from whether organisms reproduce in

848   one year or in more than one year ("classic" semelparity and iteroparity), or whether or

not organisms have a distinct life cycle that is completed according to an annual cycle or

850   not (annuality and perenniality). Consider two annual plants as an example: the

concentration of reproductive effort in time—i.e. realizing a hyper-semelparous (or

852   uniparous) reproductive strategy—is a different strategy than spreading reproduction out

over many months, even if both strategies are completed within a single year. Moreover,

854   the evolutionary and mechanistic reasons that account for seasonal behaviours—e.g.

annuality and perenniality—are distinct from those that account for the degree of parity.

856   Making these distinctions clear, both in language and in predictive models, should be an

important priority for evolutionary ecologists interested in the problem of parity.

858   Other important issues exist as well. A second question is that the extant body of

theory—much of which describes various special cases in which demographic or

860   environmental factors confer a fitness advantage on an annual-semelparous strategy over

a perennial-iteroparous one (or vice versa)—should be preserved and reworked into a

862   more general explanation of how factors affecting fitness through time determine optimal

       patterns of the distribution of risk in and among seasons. More general models should

864   consider a range of possible modes of parity. A third issue is that reproductive characters

       of long-lived semelparous species are generally easier to model than characters of short-

866   lived species, and while environmental heterogeneity plays an important role determining

       the optimal allocation of reproductive effort in annual semelparous species, long-lived

868   semelparous species can afford to be "choosier" about when they reproduce, and

       therefore have been shown to more closely approximate model predictions. This may be

870   especially true when, as in many long-lived perennial-iteroparous species, the

       relationship between age and cost of reproduction is nonlinear. Thus, developing models

872   that accurately model the fitness dynamics of short-lived semelparous species should be a

       priority. Fourth, intraspecific differences in life-history strategy, particularly between

874   populations inhabiting dissimilar environments, can confound the degree to which

       empirical studies can test predictions of *a priori* models or parameterize them. Additional

876   empirical comparisons of different modes of parity should therefore be as general as

       possible, and incorporate as many points along the continuum of modes of parity as

878   possible, in order to maximize generalizability. Last, new models of modes of parity

       should, on a system-by-system basis, attempt to account for the underlying mechanisms

880   that determine the timing and nature of the allocation of reproductive effort. Because

       modes are composite traits, integrating the molecular mechanisms that underlie many

882   traits into a single model is not a simple task. Moreover, even orthologous genes with

       may have dramatically different effects in closely related species, and this

884   unpredictability may considerably complicate the process of mechanistically modelling of

modes of parity. Despite the considerable challenge that it poses, integrating molecular

886   ecological studies of the fitness consequences of different genotypes with theoretical

mathematical models should be an important priority in the medium- to long-term future,

888   and would represent an important area of consilience between molecular and theoretical

ecology.

890

VI. ACKNOWLEDGEMENTS

898   **VII. TABLES**

Plant Order	Families	Estimated Number of Species	Class	Exemplar Species	Semelparous Species Present	Iteroparous Species Present	Notes	Reference
Acorales	1	2	M	*Acorus calamus*		x	-	(Kew World Checklist)
Alismatales	13	4500	M	*Anthurium andraeanum*	x	x	facultative semelparity	(Haggard and Tiffney, 1997; Haston et al., 2009)
Amborellales	1	1	-	*Amborella trichopoda*	x		-	(Kew World Checklist, 2017)
Apiales	7	5500	D	*Daucus carota*	x	x	facultative semelparity in Heracleum spp.	(Chandler and Plunkett, 2004; Kew World Checklist, 2017)
Aquifoliales	5	600	D	*Ilex aquifolium*	x	x	-	(Kew World Checklist, 2017)
Arecales	1	2600	M	*Cocos nucifera*	x	x	facultative semelparity in *Rhopalostylis sapida*	(Silvertown et al., 1993)
Asparagarles	14	36000	M	*Asparagus officinalis*	x	x	facultative semelparity in *Yucca whipplei*	(Keeley et al., 1986)
Asterales	11	27500	D	*Helianthus annuus*	x	x	facultative iteroparity in *Lobelia inflata*	(Hughes and Simons, 2014b; c)
Austrobaileyales	3	100	NA	*Illicium verum*		x	-	(Palmer et al., 2004)
Berberidopsidales	2	6	D	*Berberidopsis corallina*		x	-	(Kew World Checklist, 2017)
Brassicales	17	4500	D	*Brassica oleracea*	x	x	"perpetual flowering" under genetic control (*Arabis alpina*); phenotypically plastic semelparity in *Brassica campestris*	(Biswas and Mandal, 1987; Wang, Farrona, Vincent, Fornara, et al., 2009; Kew World Checklist, 2017) Albani PEP1; 2: Biswas, A. K., and S. K. Mandal. "Regulation of monocarpic senescence of Brassica campestris by the developing pods." Physiologia Plantarum 71.1 (1987): 89-94.
Bruniales	2	80	D	*Desfontainia spinosa*	x	x	fire-dependent facultative parity (Bruniaceae spp.)	(van Wilgen and Forsyth, 1992) Van Wilgen and Forsyth (1992)
Buxales	3	120	D	*Buxus sempervirens*		x	-	(Kew World Checklist, 2017)

Order								
Canellales	2	136	D	*Canella winteriana*	x	x	-	(Kew World Checklist, 2017)
Caryophyllales	33	11000	D	*Silene dioica*	x	x	Plasticity of iteroparous reproduction in *Ferocactus wislizeni*; variation in many long-lived Cactaceae perennial spp.; similar changes in Buckwheat (Polygonaceae)	(Bowers, 2000; Song et al., 2013)
Celastrales	2	1300	D	*Celastrus orbiculatus*		x	-	(Kew World Checklist, 2017)
Ceratophyllales	1	10	-	*Ceratophyllum submersum*	x	x	plasticity of iteroparous life histories in European hornworts	(Bisang et al., 2008)
Chloranthales	1	75	-	*Sarcandra glabra*		x	-	(Kew World Checklist, 2017)
Commelinales	5	850	M	*Commelina communis*	x	x	Phenotypically plastic semelparity in genus Commelina; varies from near-uniparity to extended semelparity	(Faden, 1993, 2006)
Cornales	6	600	D	*Hydrangea macrophylla*	x	x	Facultative iteroparity in stickleaf spp.	(Keeler, 1987)
Crossosomatales	7	80	D	*Crossosoma bigelovii*		x		(Kew World Checklist, 2017)
Cucurbitales	8	2600	D	*Begonia obliqua*	x	x	facultative iteroparity among cultivated begonias	(De Wilde, 2010)
Dilleniales	1	400	D	*Hibbertia stellaris*	x	x	facultative semelparity in Hibbertia spp	(Stebbins and Hoogland, 1976)
Dioscoreales	3	1050	M	*Dioscorea rotundata*		x	-	(Kew World Checklist, 2017)
Dipsacales	2	1100	D	*Lonicera periclymenum*		x	-	(Kew World Checklist, 2017)

Order	#	#	Type	Example species	x	x	Notes	Reference
Ericales	25	11000	D	*Vaccinium macrpcarpon*	x	x	Facultative semelparity and facultative iteroparity in Impatiens spp.	(Vervoort et al., 2011)
Escalloniales	1	130	D	*Escallonia bifida*	x	x	-	(Kew World Checklist, 2017)
Fabales	4	20000	D	*Pisum sativum*	x	x	facultative iteroparity in many spp.	(Nichols et al., 2007)
Fagales	7	2000	D	*Quercus alba*		x	-	(Kew World Checklist, 2017)
Garryales	2	18	D	*Garrya congdonii*		x	-	(Kew World Checklist, 2017)
Gentianales	5	16000	D	*Gentiana verna*	x	x	plasticity of iteroparous reproduction in long lived perennial *Frasera caroliniensis*	(Threadgill et al., 1981)
Geraniales	5	900	D	*Geranium rotundifolium*	x	x	-	(Kew World Checklist, 2017)
Gunnerales	2	55	D	*Gunnera manicata*	x	x	facultative semelparity in *Gunnera herteri*	(Wanntorp et al., 2002)
Huerteales	4	20	D	*Huertea cubensis*		x	-	(Kew World Checklist, 2017)
Lamiales	20	24000	D	*Lamium purpureum*	x	x	-	(Kew World Checklist, 2017)
Laurales	7	2500	D	*Laurus nobilis*		x	-	(Kew World Checklist, 2017)
Liliales	10	1300	M	*Lilium candidum*	x	x	Many perennial Agave spp. have substantial phenotypic plasticity in parity	(Nobel, 1977; Arizaga and Ezcurra, 1995; Rocha et al., 2005)
Magnoliales	6	5000	-	*Magnolia virginiana*	x	x	-	(Kew World Checklist, 2017)
Malpighiales	35	16000	D	*Malpighia glabra*	x	x	-	(Kew World Checklist, 2017)
Malvales	9	6000	D	*Malva sylvestris*	x	x	-	(Kew World Checklist, 2017)
Myrtales	9	11000	D	*Myrtus communis*	x	x	-	(Kew World Checklist, 2017)
Nymphaeales	3	70	-	*Nymphaea lotus*		x	-	(Kew World Checklist, 2017)
Oxalidales	7	1800	D	*Oxalis acetosella*	x	x	-	(Kew World Checklist, 2017)
Pandanales	5	1300	M	*Pandanus utilis*		x	-	(Kew World Checklist, 2017)

Order	Families	Species	Class	Type species				Reference
Paracryphiales	1	36	D	*Paracryphia alticola*		x	-	(Kew World Checklist, 2017)
Petrosaviales	1	5	M	*Petrosavia sakuraii*		x	-	(Kew World Checklist, 2017)
Picramniales	1	65	D	*Picramnia xalapensis*		x	-	(Kew World Checklist, 2017)
Piperales	4	4000	-	*Piper nigrum*	x	x	facultative semelparity in *Piper pellucida*	(Wanke et al., 2006)
Poales	16	18000	M	*Zea mays*	x	x	facultative iteroparity and variable iteroparity in bamboo, wheat	(Franklin, 2004; Montti et al., 2011; Baum et al., 2013)
Proteales	3	1000	D	*Protea caffra*		x	-	(Kew World Checklist, 2017)
Ranunculales	7	2800	D	*Ranunculus occidentalis*	x	x	phenotypically plastic parity in many Meconopsis spp.	(Sulaiman and Babu, 1996)
Rosales	9	7700	D	*Rosa blanda*	x	x	-	(Kew World Checklist, 2017)
Sabiales	1	100	D	*Sabia campanulata*		x	-	(Kew World Checklist, 2017)
Santalales	7	1000	D	*Santalum ellipticum*		x	-	(Kew World Checklist, 2017)
Sapindales	9	5700	D	*Acer saccharum*		x	-	(Kew World Checklist, 2017)
Saxifragales	16	2500	D	*Saxifraga stellaris*	x	x	*Saxifraga longifolia* shows phenotypically plastic parity	(García, 2003)
Solanales	5	4000	D	*Solanum tuberosum*	x	x	plasticity of long-term monocarpic reproduction in Petunia spp.	(Laroche and Bousquet, 1999)
Trochodendrales	1	2	D	*Trochodendron aralioides*		x	-	(Kew World Checklist, 2017)
Vitales	1	770	D	*Vitus vinifera*		x	-	(Kew World Checklist, 2017)
Zingiberales	8	2100	D	*Zingiber officianale*	x	x	plasticity of mode of parity in Ensete spp.	(Kirchoff, 1992; Birmeta et al., 2004)
Zygophyllales	2	300	D	*Zygophyllum album*	x	x	-	(Kew World Checklist, 2017)

900 **Table 1.** Angiosperm orders show substantial diversity in mode of parity. Data is shown for all 59 plant orders from the APG III system. Class = (M) monocot or (D) dicot. Marks indicate whether the indicated reproductive strategy is present in that order.

Focal Species	Clade	Continuously varying traits identified	Facultative Iteroparity	Facultative Semelparity	Continuous Variation in Parity	Phenotypically Plastic Parity	Reference
Acer negundo	Angiosperm	timing of reproduction				x	(Lamarque et al., 2015)
Agave celsii, Agave difformis	Angiosperm	timing of reproduction; reproductive effort			x	x	(Rocha et al., 2005)
Allogamus uncatus	Insect	timing of reproduction; duration of reproduction			x	x	(Shama and Robinson, 2009)
Alosa sapidissima	Fish	timing of reproduction; clutch size		x	x	x	(Leggett and Carscadden, 1978)
Amblyrhychus cristatus	Reptile	timing of reproduction			x	x	(Vitousek et al., 2010)
Antechinus stuartii	Mammal	adult mortality	x		x		(Fisher and Blomberg, 2011)
Arabidopsis lyrata	Angiosperm	timing of reproduction; duration of reproduction			x		(Remington et al., 2015)
Arabis fecunda	Angiosperm	reproductive effort			x	x	(Lesica and Shelly, 1995)
Bambusa narnhemica	Angiosperm	timing of reproduction			x		(Franklin, 2004)
Beta vulgaris	Angiosperm	reproductive effort				x	(Letschert, 1993; Hautekèete et al., 2001, 2002, 2009)
Boreogadus saida	Fish	adult mortality; reproductive effort			x		(Nahrgang et al., 2014)
Botryllus sclosseri	Tunicate	timing of reproduction, clutch size	x		x	x	(Grosberg, 1988; Harvell and Grosberg, 1988)
Bradybaena pellucida	Gastropod	duration of reproduction			x	x	(Nyumura and Asami, 2015)

Species	Group	Trait					Reference
Cynodonichthys brunneus, Cynodonichthys magdalenae, Cynodonichthys kuelpmanni, Anablepsoides immaculatus, and *Laimosemion frenatus*	Fish	timing of reproduction; diapause length		x	x	x	(Varela-Lasheras and Van Dooren, 2014)
Daphnia galeata	Crustacean	timing of reproduction			x	x	(Henning-Lucass et al., 2016)
Daucus carota	Angiosperm	timing of reproduction			x	x	(Lacey, 1988)
Digitaria californica	Angiosperm	juvenile mortality			x		(Smith et al., 2000)
Dosidicus gigas	Mollusc	timing of reproduction; duration of reproduction	x		x	x	(Hoving et al., 2013)
Emoia atroscostata	Reptile	timing of reproduction			x		(Alcala and Brown, 1967)
Erpobella octoculata	Leech	adult mortality; reproductive effort	x		x	x	(Maltby and Calow, 1986)
Erysimum capitatum	Angiosperm	timing of reproduction		x	x		(Kim and Donohue, 2011)
Eulamprus tympanum	Reptile	clutch size; timing of reproduction			x	x	(Doughty and Shine, 1997)
Forficula auricularia	Insect	timing of reproduction				x	(Meunier et al., 2012)
Fucus serratus; Himanthalia elongata	Algae	duration of reproduction			x		(Brenchley et al., 1996)
Gaimardia bahamondei	Bivalve	timing of reproduction; duration of reproduction	x		x	x	(Chaparro et al., 2011)
Galaxias maculatus	Fish	timing of reproduction	x			x	(Stevens et al., 2016)
Gasterosteus aculeatus	Stickleback	timing of reproduction; reproductive effort		x	x	x	(Snyder, 1991; Bell and Foster, 1994; Baker et al., 2008, 2015)
Gracilinanus microtarsus	Mammal	male adult mortality	x		x	x	(Kraaijeveld et al., 2003; Martins et al., 2006)
Idiosepius pygmaeus	Cephalopod	timing of reproduction	x		x		(Lewis and Choat, 1993; Nesis, 1996)
Ligia cinerascens	Crustacean	adult mortality; timing of reproduction	x	x	x	x	(Furota and Ito, 1999)

Species	Taxon	Trait					Reference
Lobelia inflata	Angiosperm	timing of reproduction; duration of reproduction	x		x	x	(Hughes and Simons, 2014 a,b,c)
Loligo vulgaris	Cephalopod	timing of reproduction; clutch size	x		x		(Melo and Sauer, 1999; Sauer et al., 1999)
Mallotus villosus	Fish	adult mortality; timing of reproduction		x	x	x	(Christiansen et al., 2008)
Marmosops paulensis	Mammal	female adult mortality	x		x	x	(Leiner et al., 2008)
Mimulus guttatus	Angiosperm	duration of flowering			x	x	(Van Kleunen, 2007)
Misumena vatia	Arachnid	juvenile mortality			x	x	(Morse, 1994; Morse and Stephens, 1996)
Nautilus spp.	Cephalopod	timing of reproduction; timing of senescence	x		x	x	(Ward, 1983, 1987)
Oenothera deltoides; Oenothera pallida	Angiosperm	timing of reproduction; adult mortality	x	x	x		(Evans et al., 2005)
Oncorhymchus mykiss	Fish	reproductive effort	x		x	x	(Seamons and Quinn, 2010)
Oncorhynchus nerka	Fish	timing of reproduction				x	(Hendry et al., 2004)
Oncorhynchus tshawytscha	Fish	adult mortality	x			x	(Unwin et al., 1999)
Onopordum illyricum	Angiosperm	timing of reproduction		x			(Rees et al., 1999)
Opisthoteuthis agassizii, Opistho-teuthis grimaldii and *Grimpoteuthis glacialis*	Cephalopod	timing of reproduction; reproductive effort			x		(Aldred et al., 1983; Villanueva, 1992; Vecchione et al., 1998)
Panicum bisulcatum, Cyperus michelianus, Fimbristylis miliacea, and *Eclipta prostrata*	Angiosperm	timing of reproduction; duration of reproduction			x	x	(Song et al., 2015)
Parantechnius apicalis	Mammal	adult mortality		x		x	(Wolfe et al., 2004)
Plecoglossus altivelis	Fish	timing of reproduction; reproductive effort	x		x	x	(Iguchi, 1996; Iguchi and Tsukamoto, 2001)
Puya raimondii	Angiosperm	reproductive effort		x	x		(Jabaily and Sytsma, 2013)
Rana arvalis	Frog	timing of reproduction				x	(Richter-Boix et al., 2014)
Sasa senanensis, Sasa kurilensis, and *Sasa palmata*	Angiosperm	timing of reproduction; reproductive effort	x	x		x	(Mizuki et al., 2014)

Species	Group	Traits					Reference
Sepia officinalis	Cephalopod	adult mortality; timing of reproduction; clutch size; timing of senescence	x		x	x	(Boletzky, 1988; Rocha et al., 2001)
Stegodyphus lineatus	Arachnid	adult mortality; timing of reproduction			x	x	(Schneider and Lubin, 1997)
Sthenoteuthis oualaniensis	Cephalopod	timing of reproduction	x				(Rocha et al., 2001)
Strix uralensis	Bird	timing of reproduction				x	(Brommer et al., 2012)
Uta stansburiana	Reptile	duration of reproduction,		x	x	x	(Tinkle, 1969)
Verbascum thapsis	Angiosperm	timing of reproduction			x		(Reinartz, 1984)
Wyeomyla smithii	Angiosperm	timing of reproduction			x	x	(Bradshaw, 1986)
Xerolenta obvia	Gastropod	timing of reproduction	x		x	x	(Lazaridou and Chatziioannou, 2005)
Xeropicta derbentina	Gastropod	timing of reproduction	x		x	x	(Aubry et al., 2005; Kiss et al., 2005)
Yucca whipplei	Angiosperm	reproductive effort		x	x		(Huxman and Loik, 1997)

902   Table 2. Species known to display facultative semelparity, facultative iteroparity, a continuum of modes of parity, or phenotypic plasticity with respect to mode of parity.

Study Organism	Clade	Gene /QTL	Traits	Reference
Actinidia chinensis	Angiosperm	caroteinoid cleavage dioxygenase 8 (CCD8)	branch development; timing of senescence	(Ledger et al., 2010)
Aedes aegypti, A. albopictus	Insect	cytochrome P450 gene 6Z6 (CYP6Z6), 6N12 (CYP6N12), and M9 (CYP9M9)	juvenile mortality	(Kim and Muturi, 2012)
Arabidopsis lyrata	Angiosperm	LG3, LG4	developmental timing of reproductive transitions; branchiness	(Leinonen et al., 2013; Remington et al., 2013, 2015)
Arabidopsis thaliana	Angiosperm	Early day-length insensitive (EDI)	response to vernalization; timing of flowering	(Alonso-Blanco et al., 1998)
Arabidopsis thaliana	Angiosperm	FLC	timing of initiation of reproduction	(Bastow et al., 2004; Caicedo et al., 2004; Kim et al., 2007; Aikawa et al., 2010; Deng et al., 2011)
Arabidopsis thaliana	Angiosperm	FRI	timing of initiation of reproduction	(Le Corre et al., 2002; Stinchcombe et al., 2004; Shindo et al., 2005; Méndez-Vigo et al., 2011)
Arabidopsis thaliana	Angiosperm	DOG1	seed dormancy; timing of initiation of reproduction	(Chiang et al., 2011, 2013)
Arabidopsis thaliana; Pisum sativum	Angiosperm	More axillary growth (MAX4); Ramosus1 (RMS1)	axillary shoot outgrowth; timing of outgrowth	(Sorefan et al., 2003)
Arabis alpina	Angiosperm	PEP1	timing of initiation of reproduction; perenniality	(Wang, Farrona, Vincent, Fornara, et al., 2009; Albani et al., 2012; Castaings et al., 2014b)
Brachionus plicatilis	Rotifer	small heat shock protein 1 (shsp-1), shsp-2, shsp-3, shsp-4	dormancy; juvenile mortality	(Denekamp et al., 2011)
Colias eutytheme, C. philodice	Insect	phosphoglucose isomerase (PGI)	lifespan, fecundity	(Watt, 1983; Watt et al., 1983)
Conregonus clupeaformis	Fish	*Salmo salar* zonadhesin-like	fecundity	(Nolte et al., 2009)
Drosophila melanogaster	Insect	Met	fecundity, timing of initiation of reproduction	(Flatt and Kawecki, 2004)

Drosophila melanogaster	Insect	Juvenile hormone (JH), TOR	lifespan, timing of transition to adulthood	(Tatar et al., 2001, 2003; Kapahi et al., 2004; Katewa and Kapahi, 2011)
Gadus morhua	Fish	Growth hormone 1	timing of juvenile maturation	(Hemmer-Hansen et al., 2014)
Gryllus firmus	Insect	Juvenile hormone (JH)	fecundity	(Zera and Huang, 1999; Zhao and Zera, 2002)
Haliotis refescens	Mollusc	engrailed, aragonite protein 24k Da (ap24)	juvenile mortality	(Zippay et al., 2010)
Heliocidaris erythrogamma	Echinoderm	Abopec, Brn1, Brn2, Brn4	feeding behaviour; timing of initiation of reproduction	(Israel et al., 2016)
Hordeum vulgare	Angiosperm	QSD1	seed dormancy	(Sato et al., 2016)
Ichthyomyzon castaneus, I. fossor	Lamprey	insulin-like growth factor 1 receptor (igf1r), cytochrome c oxidase subunit III (coIII)	fecundity	(Spice et al., 2014)
Lactuca sativa	Angiosperm	DOG1	seed dormancy; timing of initiation of reproduction	(Huo et al., 2016)
Miletaea cinxia	Insect	phosphoglucose isomerase (PGI)	lifespan, fecundity	(Klemme and Hanski, 2009; Saastamoinen et al., 2009)
Miletaea cinxia	Insect	troponin-t (TNT)	timing of transition to adulthood	(Marden et al., 2008)
Mimulus guttatus	Angiosperm	More axillary growth (MAX)	axillary shoot outgrowth; timing of outgrowth	(Baker et al., 2012)
Mimulus guttatus; M. nasutus	Angiosperm	-	timing of reproduction; reproductive allocation	(Hall et al., 2006)
Oncorhynchus kisutch, O. keta, O. gorbuscha	Fish	Clock, Cytochrome	timing of juvenile maturation	(O'Malley et al., 2010)
Oncorhynchus mykiss	Fish	Omy5 loci, including OC6, OC8, OC14, OC20, OC21, and OC30	anadromy, timing of smoltification	(Nichols et al., 2008; Pearse et al., 2014)
Oncorhynchus mykiss	Fish	Clock	spawning time	(Leder et al., 2006)

Oncorhynchus mykiss	Fish	One3ASC, One19ASC	biannual spawning	(Colihueque et al., 2010)
Oncorhynchus mykiss, Oncorhynchus kitsuch	Fish	17a,20b-dihy- droxy-4-prengnen-3-one	timing of senescence	(Barry et al., 2010)
Petromyzon marinas, Lampetra appendix	Lamprey	Gonadotropin-releasing hormone-I (GnRH-I) and –III (GnRH-III)	timing of transition to adulthood	(Youson et al., 2006)
Petunia hybrida	Angiosperm	Decreased apical dominance 1 (DAD1), MAX1, MAX2, CCD7, CCD8	axillary shoot outgrowth; timing of and reproductive effort allocated to floral development	(Snowden, 2005; Drummond, 2012)
Rhagoletis pomonella	Insect	jetlag (jet), clockwork orange (cwo), PAR-domain protein 1 (Pdp1)	timing of diapause termination	(Ragland et al., 2011)
Sarcophaga crassipalpis	Insect	heat shock protein 23 (Hsp23), Hsp70, Hsp90, lipid storage protein (LSP)-1, LSP-2	timing of diapause termination; timing of reproduction; reproductive effort	(Rinehart et al., 2000, 2007; Hahn et al., 2008)
Thlaspi caerulescens	Angiosperm	Thlc1, Thlc2, Thlc3	fecundity, timing of initiation of reproduction	(Jiménez-Ambriz et al., 2007)

906   Table 3. Genes and QTLs regulating continuously-expressed traits linked to parity.

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