

Reproductive senescence: new perspectives in the wild

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ABSTRACT

According to recent empirical studies, reproductive senescence, the decline in reproductive success with increasing age, seems to be nearly ubiquitous in the wild. However, a clear understanding of the evolutionary causes and consequences of reproductive senescence is still lacking and requires new and integrative approaches. After identifying the sequential and complex nature of female reproductive senescence, we show that the relative contributions of physiological decline and alterations in the efficiency of parental care to reproductive senescence remain unknown and need to be assessed in the light of current evolutionary theories of ageing. We demonstrate that, although reproductive senescence is generally studied only from the female viewpoint, age-specific female reproductive success strongly depends on male–female interactions. Thus, a reduction in male fertilization efficiency with increasing age has detrimental consequences for female fitness. Lastly, we call for investigations of the role of environmental conditions on reproductive senescence, which could provide salient insights into the underlying sex-specific mechanisms of reproductive success. We suggest that embracing such directions should allow building new bridges between reproductive senescence and the study of sperm competition, parental care, mate choice and environmental conditions.

Key words: age-specific trade-offs, ejaculate quality, environmental conditions, life-history evolution, maternal effects, reproductive ageing, sperm competition, sexual selection, parental care.

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I. INTRODUCTION

Understanding how age impacts individual performance and fitness is a long-standing question in evolutionary ecology (Monaghan *et al.*, 2008; Fletcher & Selman, 2015). Among phenotypic traits that show senescence in the wild (e.g. Nussey

et al., 2009; Jégo *et al.*, 2014; Hammers *et al.*, 2015), age-related declines in survival and reproduction (coined actuarial and reproductive senescence, respectively) are indisputably the most studied (see Nussey *et al.*, 2013, for a review), probably because survival and reproduction correspond to direct components of individual fitness (Bouwhuis *et al.*, 2012; Kowald

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& Kirkwood, 2015). Thanks to the increasing availability of longitudinal studies based on individuals of known age monitored from birth to death (Clutton-Brock & Sheldon, 2010), there is now compelling evidence that actuarial and reproductive senescence is the rule rather than the exception in free-ranging populations of vertebrates (Nussey *et al.*, 2013).

Fifty years ago, William D. Hamilton proposed a robust theoretical framework demonstrating that the decrease in the force of natural selection inevitably leads to actuarial senescence in any age-structured population (Hamilton, 1966). However, his model did not provide any explicit prediction about reproductive senescence. More specifically, while Hamilton (1966) predicted that actuarial senescence must occur in any age-structured population and should start at the age of first reproduction, he also stated that the timing and magnitude of reproductive senescence is much more difficult to predict. Although some case studies have recently pointed out that reproductive senescence can be uncoupled from actuarial senescence (e.g. Hayward *et al.*, 2015), reproductive senescence is usually grounded in the same theoretical framework used to explain actuarial senescence (Lemaître *et al.*, 2015), which includes antagonistic pleiotropy (Williams, 1957), the principle of allocation (Cody, 1966), and the disposable soma theory of ageing (Kirkwood, 1977). These theories share the common prediction that greater allocation to growth or reproduction during early life should be associated with a much steeper decline in fitness (i.e. reproductive success, survival, or both) during late life. However, while it is helpful to understand the diversity of senescence patterns observed in the wild (Jones *et al.*, 2014), whether greater early allocation to growth or reproduction predominantly impacts survival or reproductive performance at late ages is currently unknown (but see Section V).

While actuarial senescence focuses on whether or not an individual is alive or not at a given age, reproductive senescence involves a full array of traits that covary in complex ways. Indeed, age-specific reproductive success of a given individual at each reproductive event depends on a set of traits that influence the final reproductive output sequentially (Clutton-Brock, 1991). Historically, reproductive senescence has been measured as the decrease in female reproductive rate (using m_x , the number of daughters alive at birth that are produced by a female of age x) with increasing age (Emlen, 1970), likely because m_x is a standard life table statistic traditionally recorded in population biology (Skalski, Ryding & Millspaugh, 2005). However, other metrics are also used to assess age-specific changes in female reproductive performance. Some of these are direct components of reproductive success such as birth rates (e.g. McAdam *et al.*, 2007), juvenile survival (e.g. Packer, Tatar & Collins, 1998) or clutch/litter size (e.g. Balbontin *et al.*, 2012) while others indirectly influence reproductive success through offspring survival, such as offspring mass (e.g. Sharp & Clutton-Brock, 2010) or offspring birth or laying date (e.g. Nussey *et al.*, 2006). Thus, although reproductive success is generally defined as the number of offspring alive at

the end of the period of maternal allocation (Lack, 1947), reproductive senescence has often been studied using a wide diversity of direct and indirect metrics. Strikingly, when age-specific changes across different components of female reproductive success are analysed simultaneously within a given population, they display heterogeneous patterns of senescence (e.g. Hayward *et al.*, 2013; Berger *et al.*, 2015b). We highlight below how such discrepancies emphasize the need for an integrative approach that accounts for the sequential nature of reproductive senescence.

When reviewing the literature on reproductive senescence, it appears that empirical evidence of reproductive senescence in the wild mostly relies on studies focused on females (Nussey *et al.*, 2013). However, the limited information gained from long-term studies of paternity data provides firm support for reproductive senescence in free-ranging males (Table 1). We emphasize here the importance of thorough approaches of age-specific reproductive performance in males. We first detail how the scarcity of age-dependent data on male reproductive success prevents accurate identification of the drivers of reproductive senescence. Then, we propose new research directions that could allow identification of the evolutionary implications of male reproductive senescence in the wild, notably for females.

Overall, our work proposes several exciting and novel research avenues that should clarify, and potentially change, our current understanding of reproductive senescence in the wild. Although an uncoupling between reproductive senescence and actuarial senescence schedules can potentially create the opportunity for a period of post-reproductive lifespan (Cohen, 2004; Croft *et al.*, 2015), this topic is beyond the scope of the present review. Indeed, everything else being equal, post-reproductive lifespan can simply result from extended longevity rather than shortened reproductive life or accelerated reproductive senescence (Alberts *et al.*, 2013; Croft *et al.*, 2015). In addition, while reproductive senescence is widespread in vertebrates (Nussey *et al.*, 2013) post-reproductive lifespan seems to be restricted to some mammalian species (e.g. Nichols, Zecherle & Arbuckle, 2016, but see Ellison & Ottinger, 2014, for a discussion in birds). Finally, evidence of reproductive senescence reported so far in free-ranging populations is mostly based on long-term monitoring of mammals or birds (Nussey *et al.*, 2013) and the case studies we review here are thus logically focused on these vertebrate classes. Nevertheless, reproductive senescence has also been detected in reptiles (e.g. Massot *et al.*, 2011; Warner *et al.*, 2016), fishes (e.g. Morbey, Brassil & Hendry, 2005), and invertebrates (e.g. Zajitschek *et al.*, 2009), and the research questions we discuss are relevant to all animal species.

II. THE SEQUENTIAL NATURE OF REPRODUCTIVE SENESCENCE

(1) From oocyte production to maternal care

In vertebrate females, the commonly reported decline in the quantity of offspring produced with increasing age

Table 1. Studies investigating age-related decline in male reproductive performance for free-ranging populations of male birds and mammals. (A) Senescence in reproductive success, (B) senescence in pre-copulatory sexual traits, and (C) senescence in post-copulatory sexual traits. The 'Senescence' column indicates whether the study provides evidence for a decline in reproductive traits at old ages (yes) or not (no). The column 'Data' indicates whether the study is longitudinal (L) or transversal (T). When provided, we retrieved the age at the onset of senescence from studies reporting reproductive senescence

Species	Senescence	Data	Onset	References
(A) Reproductive success				
Birds				
Barnacle goose (<i>Branta leucopsis</i>)	No	L	NA	Forslund & Larsson (1992)
Black grouse (<i>Tetrao tetrix</i>)	No	L	NA	Kervinen, Lebigre & Soulsbury (2016)
Blue-footed booby (<i>Sula nebouxi</i>)	Yes	L; L	9; 10	Velando, Drummond & Torres (2006) and Kim <i>et al.</i> (2011)
Cassin's auklet (<i>Phychostrampus aleuticus</i>)	No	L	NA	Pyle, Sydeman & Hester (2001)
Coal tit (<i>Parus ater</i>)	No	T	NA	Schmoll <i>et al.</i> (2007)
Common guillemot (<i>Uria aalge</i>)	Yes	L	—	Reed <i>et al.</i> (2008)
Coot (<i>Fulica atra</i>)	No	T	NA	Brinkhof <i>et al.</i> (1993)
Lanced-tailed manakin (<i>Chiroxiphia lanceolata</i>)	Yes	L	8.6	DuVal (2012)
Merlin (<i>Falco columbarius</i>)	No	L	NA	Espie <i>et al.</i> (2000)
New Zealand hibi (<i>Notionystis cincta</i>)	Yes	L	6	Brekke <i>et al.</i> (2013)
Purple martin (<i>Progne subis</i>)	Yes	T	7	Tarof <i>et al.</i> (2012)
Short-tailed shearwater (<i>Puffinus tenuirostris</i>)	Yes	L	NA	Bradley, Wooller & Skira (2000)
Snow petrel (<i>Pogadroma nivea</i>)	No	L	NA	Angelier <i>et al.</i> (2007)
Song sparrow (<i>Melospiza melodia</i>)	Yes	L; L	6; 7	Losdat <i>et al.</i> (2016) and Keller, Reid & Arcese (2008)
Tree swallow (<i>Tachycineta bicolor</i>)	Yes	L	3	Vleck, Vleck & Palacios (2011)
Wandering albatross (<i>Diomedea exulans</i>)	Yes	L; L	[16–27]; 23	Froy <i>et al.</i> (2013) and Patrick & Weimerskirch (2015)
Willow tit (<i>Parus montanus</i>)	No	L	NA	Orell <i>et al.</i> (1999)
Wood Thrush (<i>Hylocichla mustelina</i>)	Yes	L	6	Brown & Roth (2009)
Alpine ibex (<i>Capra ibex</i>)	Yes	T	11	Willisch <i>et al.</i> (2012)
African elephant (<i>Loxodonta africana</i>)	Yes	L; T	48; —	Hollister-Smith <i>et al.</i> (2007) and Rasmussen <i>et al.</i> (2008)
Bighorn sheep (<i>Ovis canadensis</i>)	Yes	L	—	Coltman <i>et al.</i> (2002)
Bison (<i>Bison bison</i>)	Yes	L; L; T	11; 14; —	Wolff (1998), Wilson, Olson & Strobeck (2002) and Mooring & Penedo (2014)
Black bear (<i>Ursus americanus</i>)	Yes	T	10	Costello <i>et al.</i> (2009)
Black rhinoceros (<i>Diceros bicornis</i>)	No	T	NA	Cain <i>et al.</i> (2014)
Columbian ground squirrel (<i>Urocyon columbianus</i>)	Yes	L	5	Raveh <i>et al.</i> (2010)
European badger (<i>Meles meles</i>)	Yes	L; L	6; 5	Carpenter <i>et al.</i> (2005) and Dugdale <i>et al.</i> (2011)
Fallow deer (<i>Dama dama</i>)	Yes	L	~5 /6	McElligott, Altwegg & Hayden (2002)
Feral cat (<i>Felis catus</i>)	No	L	NA	Ishida <i>et al.</i> (2001)
Feral horse (<i>Equus caballus</i>)	Yes	L	9	Feh (1990)
Greater sac-winged bat (<i>Saccopteryx bilineata</i>)	Yes	L	4	Greiner <i>et al.</i> (2014)
Grey seal (<i>Halichoerus grypus</i>)	No	L	NA	Lidgard, Bowen & Boness (2012)
Mountain goat (<i>Oreamnos americanus</i>)	Yes	L	8	Mainguy, Cote & Coltman (2009)
Rhesus macaque (<i>Macaca mulatta</i>)	Yes	L	11	Widdig <i>et al.</i> (2004)
Red deer (<i>Cervus elaphus</i>)	Yes	L	10	Nussey <i>et al.</i> (2009)
Roe deer (<i>Capreolus capreolus</i>)	Yes	L	8	Vampé <i>et al.</i> (2009)
Soay sheep (<i>Ovis aries</i>)	Yes	L	7	Hayward <i>et al.</i> (2015)

Table 1. Continued

Species	Senescence	Data	Onset	References
(B) Pre-reproductive sexual traits				
Birds				
Barn swallow (<i>Hirundo rustica</i>)	Yes	L	5	Balbontín <i>et al.</i> (2011)
Barn swallow (<i>Hirundo rustica</i>)	No	L	—	Galván & Møller (2009)
Barn swallow (<i>Hirundo rustica</i>)	No	L	—	Galván & Møller (2009)
Blue-footed booby (<i>Sula nebouxi</i>)	Yes	T	10	Torres & Velando (2007)
Sedge warbler (<i>Acrocephalus schoenobaenus</i>)	No	T	—	Birkhead <i>et al.</i> (1997)
Great tit (<i>Parus major</i>)	Yes	T	~4	Rivera-Gutierrez <i>et al.</i> (2012)
Great tit (<i>Parus major</i>)	No	T	—	Rivera-Gutierrez <i>et al.</i> (2012)
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	No	L	—	Forstmeier <i>et al.</i> (2006)
Collared flycatcher (<i>Ficedula albicollis</i>)	No	L	—	Evans, Gustafsson & Sheldon (2011)
Collared flycatcher (<i>Ficedula albicollis</i>)	No	L	—	Evans <i>et al.</i> (2011)
Black grouse (<i>Tetrao tetrix</i>)	Yes	L	—	Kervinen <i>et al.</i> (2015)
Black grouse (<i>Tetrao tetrix</i>)	Yes	L	—	Kervinen <i>et al.</i> (2015)
Black grouse (<i>Tetrao tetrix</i>)	Yes	L	—	Kervinen <i>et al.</i> (2015)
Black grouse (<i>Tetrao tetrix</i>)	Yes	L	—	Kervinen <i>et al.</i> (2015)
Common kestrel (<i>Falco tinnunculus</i>)	Yes	L	2	Lopez-Idiaquez <i>et al.</i> (2016)
Common kestrel (<i>Falco tinnunculus</i>)	No	L	—	Lopez-Idiaquez <i>et al.</i> (2016)
Greater flamingo (<i>Phoenicopterus roseus</i>)	Yes	T	[16–23]	Perrot <i>et al.</i> (2016)
Greater flamingo (<i>Phoenicopterus roseus</i>)	Yes	T	[16–23]	Perrot <i>et al.</i> (2016)
Greater flamingo (<i>Phoenicopterus roseus</i>)	Yes	T	[16–23]	Perrot <i>et al.</i> (2016)
Red deer (<i>Cervus elaphus</i>)	No	L	—	Kruuk <i>et al.</i> (2002)
Red deer (<i>Cervus elaphus</i>)	No	L	—	Nussey <i>et al.</i> (2009)
Red deer (<i>Cervus elaphus</i>)	Yes	L	9	Nussey <i>et al.</i> (2009)
Red deer (<i>Cervus elaphus</i>)	Yes	L	11	Nussey <i>et al.</i> (2009)
Red deer (<i>Cervus elaphus</i>)	Yes	L	10	Nussey <i>et al.</i> (2009)
Red deer (<i>Cervus elaphus</i>)	Yes	L	10	Nussey <i>et al.</i> (2009)
Red deer (<i>Cervus elaphus</i>)	Yes	T	12	Mysterud <i>et al.</i> (2005)
Moose (<i>Alces alces</i>)	Yes	T	[7.5–9.5]	Sæther & Haagenrud (1985)
Roe deer (<i>Capreolus capreolus</i>)	Yes	L	8	Vampé <i>et al.</i> (2007)
Alpine ibex (<i>Capra ibex</i>)	Yes	L	6	Von Hardenberg <i>et al.</i> (2004)
Alpine ibex (<i>Capra ibex</i>)	Yes	T	4	Giacometti, Willing & Defila (2002)
Mountain goat (<i>Oreamnos americanus</i>)	No	L	—	Manguy & Côté (2008)
Soay sheep (<i>Ovis aries</i>)	No	L	—	Hayward <i>et al.</i> (2015)
Soay sheep (<i>Ovis aries</i>)	Yes	L	5	Hayward <i>et al.</i> (2015)

Table 1. Continued

Species	Senescence	Data	Onset	References
Soay sheep (<i>Ovis aries</i>)	Yes	L	8	Hayward <i>et al.</i> (2015)
Soay sheep (<i>Ovis aries</i>)	No	L	—	Hayward <i>et al.</i> (2015)
Bison (<i>Bison bison</i>)	Yes	T	~11	Mahe & Byers (1987)
(C) Post-copulatory sexual traits				
Birds				
Barn swallow (<i>Hirundo rustica</i>)		Horn growth		
Blue-footed booby (<i>Sula nebouxi</i>)		Number of rut consorts		
Common brush-tail possum (<i>Trichosurus vulpecula</i>)		Allocation to intrasexual competition during the rut		
Mammals				
Soay sheep (<i>Ovis aries</i>)	Yes	Sperm performance	1	Møller <i>et al.</i> (2009)
Ringed seal (<i>Phoca hispida</i>)	Yes	Ejaculate quality	10	Vclando <i>et al.</i> (2011)
Spotted hyena (<i>Crocuta crocuta</i>)	No	Testes length	—	Isaac (2004)
	Yes	Testes circumference	5	Hayward <i>et al.</i> (2015)
	Yes	Testes size	13	Chambellant (2010)
	No	Composite measure of sperm quantity	—	Curren <i>et al.</i> (2013)
Spotted hyena (<i>Crocuta crocuta</i>)	No	Composite measure of sperm size	—	Curren <i>et al.</i> (2013)

(e.g. senescence in birth rate or litter/clutch size) can have multiple underlying causes. Among these, the progressive erosion of the finite pool of primary oocytes set around birth through atresia or ovulation is a key factor, at least in mammals (Gosden & Telfer, 1987) and birds (Holmes *et al.*, 2003). Such erosion is responsible for the low number of mature follicles in the ovaries at old ages, which might potentially cause dysregulation of the hypothalamic–pituitary–ovarian axis several years before the complete cessation of reproduction (see O'Connor, Holman & Wood, 1998, 2001, for reviews). This biological process might thus be particularly relevant in terms of reproductive senescence. In addition to a decreased quantity of eggs with increasing age, progressive decline in the viability of primary oocytes could account for the low reproductive performance often observed in old females (Fedigan & Pavelka, 2011), but evidence for such a ‘shelf life’ effect is still debated (Shanley & Kirkwood, 2001). In other taxa such as fishes the picture can be less straightforward since oocytes can be produced continuously throughout life although it is still possible that their quality shows signs of senescence (Finch & Holmes, 2010). Interestingly, oocyte supplies and patterns of decline can vary both among and within species (e.g. mammals: Cloutier, Coxworth & Hawkes, 2015; birds: Holmes *et al.*, 2003), but whether such differences can account for intraspecific variation in reproductive senescence in the wild is currently unknown.

Overall, we lack information on the relationship between the decline in both quantity and quality of oocytes and reproductive senescence in the wild because measuring oocyte reserves and characteristics (e.g. size, integrity) is incompatible with individual longitudinal monitoring. Such investigations require ovarian tissue to be collected, and thereby ovariectomy or autopsy (Gosden & Telfer, 1987; Vom Saal, Finch & Nelson, 1994). It is thus not surprising that most current knowledge comes from experimental studies performed in the laboratory or on captive animals, principally rodents, primates and a few bird species (mammals: Vom Saal *et al.*, 1994; birds: Holmes *et al.*, 2003).

Although the erosion of oocyte supplies constitutes one proximal cause of reproductive senescence, decreased efficiency of the reproductive machinery probably plays a greater role (Wise, Krajnak & Kashon, 1996; Holmes *et al.*, 2003). Female reproductive physiology is extremely complex (Ellison & Ottinger, 2014; Perry *et al.*, 2015) and the depreciation of many aspects of the reproductive system might compromise reproductive success, such as the pattern of hormone secretion or atrophy of the oviduct (Vom Saal *et al.*, 1994; Ottinger, Nisbet & Finch, 1995). The decrease of most reproductive functions can generally be explained by general dysregulation of the pituitary–hypothalamic–ovarian axis. Importantly, this decline in efficiency of the pituitary–hypothalamic–ovarian axis with increasing age seems to be a direct consequence of somatic deterioration (Vom Saal *et al.*, 1994), which allows reproductive senescence to be understood within the framework of evolutionary theories of ageing. According

to the disposable soma theory of ageing, individuals that allocate heavily to reproduction early in life cannot allocate as much to somatic maintenance (Kirkwood & Rose, 1991), which progressively leads to deterioration of physiological functions (notably those involved in reproduction; Kirkwood & Shanley, 2010) and ultimately promotes more rapid reproductive senescence in late adulthood. Although the study of functional reproductive senescence in the wild remains challenging, there is a real need for ecological studies of the interaction between somatic deterioration and reproductive senescence. Adult body mass or size, recorded in longitudinal studies of most taxa, might offer a reliable indicator of physiological condition and reproductive success. Recently, several studies have revealed that senescence in body mass is widespread in the wild (e.g. Weladji *et al.*, 2010; Beirne, Delahay & Young, 2015), but whether such a decline can be a reliable predictor of reproductive senescence has not been tested. In addition, collections of biological tissues such as blood samples are increasingly available from long-term population monitoring and several biomarkers such as molecular indicators of oxidative damage are now used routinely to assess the level of somatic deterioration (Selman *et al.*, 2012). In the absence of a clear picture of age-specific patterns in the reproductive machinery, whether such biomarkers could reliably indicate the global state of the reproductive system needs to be determined. If so, it would open the door to integrative studies linking somatic maintenance and reproductive senescence.

Both oocyte depletion and physiological deterioration of the reproductive system jeopardize female reproductive success at old ages. However, even if female fertility remained constant over the entire lifespan, progressive diminution of maternal care could compromise reproductive output through a decline in offspring birth mass or early growth, and thereby survival, with increasing maternal age. Such senescence in offspring phenotypic quality has now been widely reported in terms of egg or offspring mass (e.g. Sydeman & Sydeman & Emslie, 1992; Sharp & Clutton-Brock, 2010), or offspring survival (e.g. Clutton-Brock, Albon & Guinness, 1987; Ericsson *et al.*, 2001; Descamps *et al.*, 2008). When documented, declines in offspring phenotypic quality are generally interpreted as the consequences of senescence in maternal care (e.g. Ericsson *et al.*, 2001). Detailed field studies on senescence in maternal effects remain scarce although new theoretical developments suggest that this should be stronger than senescence in fertility rate (Moorad & Nussey, 2016). In addition, old females are limited in their abilities to acquire and store body reserves (Skogland, 1988; Lecomte *et al.*, 2010), which can be deleterious in terms of the amount of resources transferred to offspring. In birds and mammals, females provide care during nestling and weaning, two critical periods more costly than incubation or gestation (Drent & Daan, 1980; Gittleman & Thompson, 1988; Clutton-Brock, Albon & Guinness, 1989) and that strongly dictate offspring growth. In mammals, the quantity of nutrients provided to offspring through lactation is positively correlated with early

growth (Hinde, Power & Oftedal, 2009) and fast-growing individuals rapidly reach a body mass threshold beyond which survival during the juvenile stage is no longer condition-dependent (Dmitriew, 2011). To the best of our knowledge, no empirical study has yet investigated whether milk quantity provided by females decreases with increasing age in wild populations. However, studies in agronomy report that the milk yield provided by cows generally peaks around 6–9 years of age (Brody, 1927; Lush & Shrode, 1950) or at the fourth to fifth lactation event (Mellado *et al.*, 2011) and decreases afterwards, independently of any change in body mass (Brody, 1927). In addition to quantity, milk composition is likely to affect the fate of offspring. Milk mostly contains water, lipids, proteins, sugars and minerals such as calcium (Oftedal, 1984), and its composition influences both offspring mass and growth in wild mammals (Mellish, Iverson & Bowen, 1999). Milk composition also affects offspring survival. In Columbian ground squirrel, *Urocitellus columbianus*, a low protein content early in lactation but high from the lactation peak to late lactation is a reliable predictor of overwinter survival of offspring, independent of their body mass (Skibieli & Hood, 2015). In birds, maternal senescence can also affect both prenatal (e.g. egg quality) and post-natal (e.g. rearing capacities) components (Bogdanova, Nager & Monaghan, 2007; Beamonte-Barrientos *et al.*, 2010). The different case studies discussed in this section highlight the sequential nature of female reproduction. From oocyte production to maternal care, reproductive success is shaped by a sequence of traits that can dramatically compromise it, either in an additive or interactive way (Fig. 1).

(2) Assessing the relative fitness cost of early *versus* late reproductive failure

To illustrate the importance of considering the sequential nature of the female reproductive cycle, we performed simulations of the fitness impact of reproductive failure at different stages of the reproductive sequence in both short-lived and long-lived life histories, in the presence of reproductive costs (Fig. 2). To quantify the fitness cost of a reproductive failure occurring early (e.g. probability to ovulate) and late (e.g. offspring death at the end of the maternal care period) in the reproductive sequence, we built a pre-breeding census age-specific female-dominant demographic model (Caswell, 2001) including the cost of raising offspring on the subsequent reproduction. We used an empirical measure of female reproductive costs in terms of fecundity from red deer (*Cervus elaphus*) and Alpine marmot (*Marmota marmota*) (a decrease of about 20%; Clutton-Brock, Guinness & Albon, 1983; Hackländer & Arnold, 1999). Thus, females of a given age having given birth to an offspring that died suffer a 20% decrease in their probability of giving birth the next year, as do females that successfully raised an offspring. We assessed fitness costs of this penalty to reproductive failure by offspring loss in two markedly different life histories: short-lived *versus* long-lived species. For the sake of simplicity, we assumed that no reproductive cost in terms of survival occurred in either the short-lived

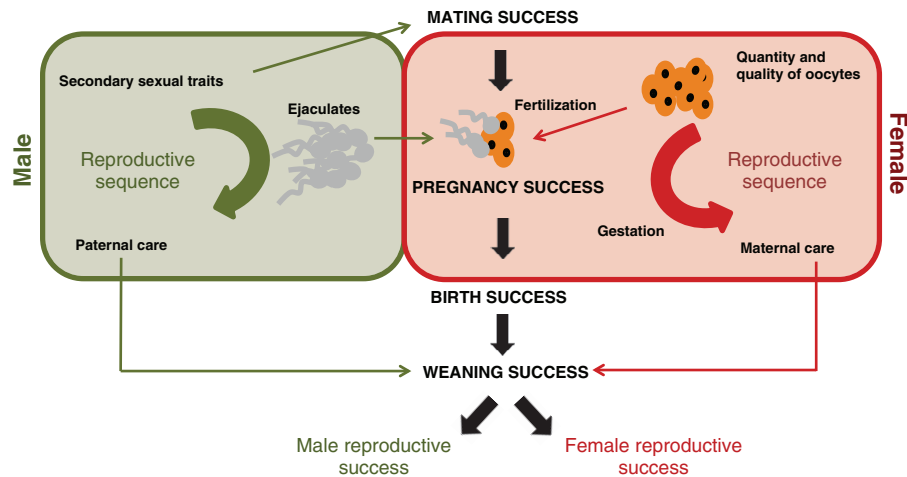


Fig. 1. Overview of sex-specific contributions to age-specific reproductive success. In both males and females reproductive success results from a complex series of events (e.g. gamete production, fertilization, gestation) involving both sexes. The probability that each of these events is a success depends on multiple phenotypic traits that potentially can all show signs of senescence.

or the long-lived life histories. Similarly, a potential trade-off between offspring number and offspring survival was not included in our simulation.

Females of the short-lived species started to give birth at 1 year of age. They all survived up to 3 years of age (annual survival rate of 1) and died just before reaching 4 years of age, meaning that the survival rate between 3 and 4 years of age was 0. We included reproductive senescence from 1 to 3 years of age: 0.8, 0.6, and 0.4 female offspring recruited by 1-, 2-, and 3-year-old females, respectively. From this life cycle, the mean female fitness estimated by the asymptotic Malthusian parameter (r ; Fisher, 1930) was 0.351 and the generation time was 1.58 years (approximating that of a great tit, *Parus major*). Females of the long-lived species started giving birth at 2 years of age. They survived up to 9 years of age (annual survival rate of 1) and died just before reaching 10 years of age, meaning that the survival rate between 9 and 10 years of age was 0. We included reproductive senescence from 2 to 9 years of age: 0.5, 0.4, 0.3, 0.2, 0.1, 0.05, 0.025 and 0.0125 female offspring recruited by 2-, 3-, 4-, 5-, 6-, 7-, 8-, and 9-year-old females, respectively. From this life cycle, the mean female fitness estimated by r was 0.135 and the generation time was 3.27 years (approximating that of a badger, *Meles meles*). We then included in both short- and long-lived life cycles the costs of the late incubation/gestation–early nestling/lactation

period, which are the most costly reproductive stages in birds and mammals (Drent & Daan, 1980; Clutton-Brock *et al.*, 1989), in two different ways. First, we assumed that all reproductive failures occurred at ovulation or early pregnancy. Only females that were successful at raising their offspring were thus subjected to reproductive costs in scenario 1. In scenario 2, we assumed that all reproductive failures occurred through offspring mortality after the lactation peak, so that females that failed at a given age also suffered from a reproductive cost in terms of reduced fecundity.

The fitness cost of reproduction under scenario 1 (i.e. no reproductive cost for females that failed the year before) was slightly above 10% in both short-lived and long-lived life histories (Table 2). By contrast, females that lost their offspring late in the reproductive process suffered from much heavier fitness costs, especially in long-lived females with a higher level of iteroparity. These simulations reveal that when the probability of failing at one of these steps increases with age, consequences in terms of reproductive senescence would be immediate. In addition, the magnitude of the fitness costs of failing depends both on the trait targeted by senescence and on the timing of the failure (Fig. 2; Table 2).

These simple demographic simulations clearly demonstrate the potential for strongly negative impacts of losing offspring late in the reproductive sequence (i.e. after the peak

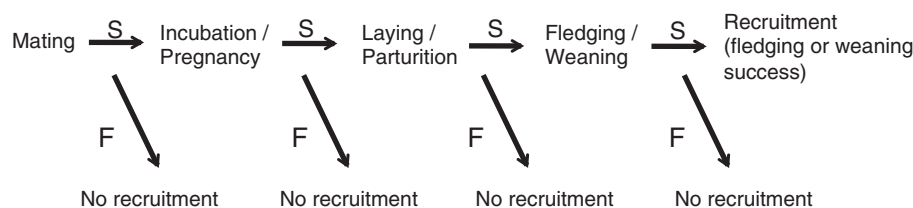


Fig. 2. Sequential nature of reproductive success in females. Reproductive success includes different stages (e.g. mating, pregnancy, birth and weaning in mammals). At each stage, a female can either succeed (S) or fail (F). The only way to recruit one offspring at the end of the reproductive cycle is to succeed at every stage. For simplicity we use a monotocous species as an example.

Table 2. Fitness costs (measured in terms of average individual fitness, r) of reproductive failure at different stages of the reproductive sequence. Scenario 1 corresponds to early reproductive failure (before birth), while scenario 2 corresponds to late reproductive failure (after lactation peak). These two scenarios include a reproductive cost in terms of reproduction in the subsequent year of 20%. Total fitness cost was measured as the proportional decrease in r and calculated between the scenario considered (1 or 2) and the situation with an identical rate of reproductive failure but no reproductive costs. Relative fitness costs were measured as the proportional decrease in r between scenario 1 and 2. Simulation results are displayed for typical short-lived and long-lived mammals (longevity of 3 and 9 years, respectively)

Scenario	Average fitness (r)	Total fitness cost (%)	Relative fitness costs (%)
Short-lived scenario 1	0.308	12.29	
Short-lived scenario 2	0.291	17.13	5.52
Long-lived scenario 1	0.120	11.36	
Long-lived scenario 2	0.094	30.47	21.57

energetic demand of lactation in mammals) when reproductive costs in terms of future reproduction occur. We should thus expect senescence to be counter-selected at a much higher intensity in late than in early reproductive stages when reproductive costs in terms of future reproduction are high. Under such conditions, we predict greater senescence in pregnancy rates than in offspring pre-weaning survival. Although we used mammals as a theoretical example in our simulation, our prediction can be tested in any species where females provide maternal care to their offspring. We expect this effect to be more pronounced in long-lived capital breeders that pay even higher fitness costs of senescence in offspring pre-weaning survival (Table 2). Further work could test this prediction using both theoretical and empirical approaches.

Results from our simulations reinforce the expectation of a terminal allocation (Weladji *et al.*, 2010) or investment (Clutton-Brock, 1984). Old reproducing females should try harder to raise their offspring successfully than young females not only because they have less chance of surviving to the next year, but also because, even if they survive, they have a lower probability of producing any offspring the next year. Unravelling the relative influences of senescence, reproductive costs, allocation to reproduction and experience constitutes an important research avenue to understand factors shaping age-dependence in maternal care.

III. REPRODUCTIVE SENESCENCE IS THE OUTCOME OF MALE–FEMALE INTERACTIONS

(1) Embracing the complexity of male reproductive senescence

It is impossible to understand variation in the probability of eggs being fertilized without simultaneously considering

both male and female reproductive expenditures. Therefore, the study of reproductive failure (and by extension, of age-dependence in reproductive failure) needs to integrate both male and female contributions (Fig. 1). As emphasized above, almost all investigations of reproductive senescence in the wild have been approached from the female viewpoint, although increasingly available paternity analyses in vertebrates have revealed clear evidence of male reproductive senescence (see Table 1). Irrespective of the mating system, the reproductive success of males is constrained by their ability to secure one or several mating opportunities and thus by their success during the pre-copulatory competition period (Darwin, 1871; Andersson, 1994). This intense competition for matings, especially in highly polygynous species, is responsible for the evolution of costly conspicuous traits and behaviours that confer competitive advantages to males allocating substantially to these traits (Clutton-Brock, 2007). Therefore, a thorough understanding of male reproductive senescence in the wild requires determination of whether male efficiency in pre-copulatory competition decreases with increasing age.

The amount of energy that males allocate to sexual competition varies depending on the mating system. In polygynous species, males often maximize their mating success by defending reproductive territories or harems (Clutton-Brock, 1989). Interestingly, in such species (e.g. large herbivores), males are less successful at controlling large territories (Vanpé *et al.*, 2009) or large harems (Nussey *et al.*, 2009) at old ages. Although current evolutionary theories of ageing do not provide clear predictions in terms of reproductive performance at old ages, declines in male pre-copulatory performance are generally studied from the viewpoint of an early- *versus* a late-life trade-off in reproductive performance (Lemaître *et al.*, 2015). Thus, red deer males allocating extensively to sexual competition by rutting during long periods and by controlling large harems show a decline in harem size after ten years of age (Lemaître *et al.*, 2014), but the exact consequences of this decline in terms of reproductive success remain to be investigated. In many taxa, males have secondary sexual traits acting either as weapons during fights with rivals or as ornaments to attract females. Such traits often influence male reproductive success positively in a wide range of taxa, from insects (e.g. Hongo, 2007) to mammals (e.g. Coltman *et al.*, 2002). A decline in weapon size could thus compromise breeding opportunities (Preston *et al.*, 2003). A few studies in laboratory (e.g. Hoikkala *et al.*, 2008; Velde *et al.*, 2012) and free-ranging conditions (reviewed in Table 1) have investigated age-specific declines in male armaments or ornaments (e.g. Kervinen *et al.*, 2015; Lopez-Idiaquez *et al.*, 2016). Interestingly, among secondary sexual traits that are positively correlated with male reproductive success in the wild, senescence occurs in foot colour intensity in the blue-footed booby (*Sula nebouxi*) (Torres & Velando, 2007) and in song consistency in the great tit (Rivera-Gutierrez, Pinxten & Eens, 2012). Conversely, antler size in male red deer and tail length in male barn swallows (*Hirundo rustica*) do not decrease at old ages

(see Nussey *et al.*, 2009; Balbontín *et al.*, 2011, respectively). Absence of senescence in secondary sexual traits was also reported in houbara bustards (*Chlamydotis undulata*) in which the level of sexual displays increased from 1 (corresponding to the age at sexual maturity of male in this bird species) to 8 years of age and then remained constant until death (Preston *et al.*, 2011). Understanding why some secondary sexual traits show signs of senescence while others do not requires an integrated approach to the ‘ageing phenotype’ that would include measures of physiological performance, health and ultimately survival [e.g. Giraudeau *et al.* (2016) for a telomere shortening cost of colouration maintenance in painted dragon, *Ctenophorus pictus*]. Such an approach would also require consideration of the environmental conditions that influence life-history strategies through changes in the quantity and quality of resources available (see Section V). Within a species, the study of senescence in secondary sexual traits can become even more complex for species displaying conspicuous ornaments. Some can show senescence while others do not (Table 1), as recently observed in a free-ranging population of Soay sheep (*Ovis aries*) (Hayward *et al.*, 2015). Such heterogeneity in senescence patterns might provide new insights into the relative importance of each sexual trait for populations in which traits in sexual competition show the slowest decline with increasing age, perhaps in response to preferential allocation to such traits at late ages (Møller & Pomiankowski, 1993; Bonduriansky *et al.*, 2008; Galván & Møller, 2009).

In most animal species, a decrease in male reproductive success with increasing age is likely to be accompanied by a reduction in male fertilization efficiency in late adulthood (Johnson & Gemmell, 2012). The reproductive cycle of males is sequential and includes two main stages, corresponding to the pre-copulatory (from the start of male–male competition to copulation) and post-copulatory (from copulation to egg fertilization) periods. These two periods are associated with two distinct types of competition, involving different organs or structures (secondary *versus* primary sexual traits). Therefore, even if a male maintains his ability to gain access to mating opportunities over the course of his life, any senescence in his abilities to fertilize eggs will compromise his reproductive success (Fig. 1). Interestingly, the decline in male ability to fertilize eggs might itself be multi-factorial because several traits defining ejaculate quality (such as sperm number per ejaculate, velocity and integrity of spermatozoa) can be increasingly impaired with age and thereby limit reproductive success at old ages (Pizzari *et al.*, 2007). Until now, this has been studied in humans (e.g. Rochebrochard & Thonneau, 2003) to investigate proximate causes of infertility. In men, ejaculate quality declines with increasing age as revealed by a meta-analysis performed on 90 clinical studies (Johnson *et al.*, 2015). Evidence of senescence in sperm quantity in other species in the wild has been reported in the American horseshoe crab, *Limulus polyphemus* (Sasson, Johnson & Brockmann, 2012), but most studies of age-specific variation in sperm-related traits focused on birds (Table 1). In the barn swallow, traits linked to

sperm swimming efficiency decrease linearly with increasing age (Møller *et al.*, 2009), while in the blue-footed booby, sperm includes more DNA damage in males older than 10 years than in middle-aged males (Velando *et al.*, 2011). In mammals, a loss in sperm quantity and/or quality at old ages has been reported from captive populations [e.g. black-footed ferret, *Mustela nigripes* (Wolf *et al.*, 2000); cheetah, *Acinonyx jubatus* (Durrant *et al.*, 2001); Asian elephant, *Elephas maximus* (Thongtip *et al.*, 2008)], where fertility is often studied for conservation purposes. Only one study investigated this question in the wild, failing to find evidence of a decline in sperm-related traits at old ages (Curren, Wedele & Holekamp, 2013, on spotted hyenas, *Crocuta crocuta*). However, their study was performed on cross-sectional data, with confounding effects of selective disappearance, possibly causing an underestimation of the intensity of senescence (Nussey *et al.*, 2008).

The examples compiled above clearly show that the study of senescence in traits defining male fertilization in the wild is still in its infancy, and we stress the importance of collecting sperm samples repeatedly throughout an individual’s life. Such protocols are evidently not straightforward because they require repeated sperm sampling from males captured during each breeding season. In mammalian species, electro-ejaculation after anaesthesia is often needed (e.g. Crosier *et al.*, 2007; Curren *et al.*, 2013; Fasel *et al.*, 2015) but other non-invasive techniques can be employed in some primates (e.g. recovery of semen sample after natural masturbating behaviour in Yakushima Macaques, *Macaca fuscata yakui*; Thomsen, 2014). Repeated semen collections are easier to obtain in passerine birds through relatively simple handling methods (Møller *et al.*, 2009). Alternatively, testes mass, a good indicator of sperm production rate is more easily measured in wild vertebrates than ejaculate quality (Ramm & Stockley, 2010), providing a reasonable measure of siring success (Preston *et al.*, 2003; Schulte-Hostedde & Millar, 2004). A recent study performed in Soay sheep revealed that testes circumference decreases from age five onwards (Hayward *et al.*, 2015). However, the relative importance of this decline on male senescence in breeding success reported in this population (Hayward *et al.*, 2015) is not known. Conversely, in birds, several studies suggest that testes mass (or volume) increases with age, which at first sight contradicts the presence of senescence in male gonad size. However, these studies are often based on two age-class comparisons typically between 1 year-old and older males (e.g. Merilä & Sheldon, 1999; Graves, 2004), precluding any reliable interpretation in terms of senescence.

In addition to providing important insights on the proximate causes of male reproductive success in the wild, longitudinal studies of senescence in ejaculate quality might stimulate the development of a theoretical framework for explaining the evolution of male reproductive senescence. To date, theoretical studies of senescence have mostly focused on actuarial senescence (Hamilton, 1966; Davison, Boggs & Baudisch, 2014) and more recently on female reproductive senescence (Cichoń, 2001; van den Heuvel, English & Uller,

2016; Moorad & Nussey, 2016). The rare studies that have documented senescence in post-copulatory traits have generally interpreted their results in the context of early- versus late-life trade-offs (Lemaître *et al.*, 2015). In houbara bustards, males displaying long sexual courtships during early life suffer from stronger senescence in ejaculate quality (Preston *et al.*, 2011), as expected under predictions shared by antagonistic pleiotropy (Williams, 1957) and disposable soma theories of ageing (Kirkwood & Rose, 1991). Finally, we emphasize that new models should incorporate both pre- and post-copulatory components of male reproductive allocation in order to predict whether age-specific allocation to pre- and post-copulatory competition is equally important in shaping senescence in male reproductive success. Such models should also consider the possibility of age-specific trade-offs between these two types of allocation (see Section IV).

(2) Consequences of male reproductive senescence on female fitness

Detailed investigations of male reproductive senescence are necessary for disentangling the relative contributions of male and female age on reproductive senescence. In domestic fowl (*Gallus gallus domesticus*), female reproductive success is negatively influenced by mating with old males that have impaired ejaculate quality (e.g. low number of sperm per ejaculation, low sperm velocity; Dean *et al.*, 2010). Offspring growth can also decrease with increasing paternal age, as in houbara bustards in which old males produce lighter offspring one month after hatching than young males (Preston *et al.*, 2015). Such effects can lead to decreased female reproductive success because in most free-ranging populations of vertebrates, the lightest juveniles are those most likely to die [e.g. Maness & Anderson (2013); see Ronget *et al.* (2017) for recent reviews in birds and mammals]. Therefore, when old females mate with old males, the senescence sometimes observed in offspring survival (e.g. mammals: Descamps *et al.*, 2008; birds: Torres, Drummond & Velando, 2011) might result from an age-related decline in female reproductive performance but might also be due to poor-quality DNA of an old male germ line. There is now a need to investigate whether detrimental effects of old paternal age are common in the wild and to quantify precisely their contribution to reproductive senescence. Interestingly, if the deleterious effects of advanced male age on female fitness are widespread, we can predict that some specific adaptations in female reproductive behaviour and physiology might have evolved to counteract the deleterious effects of impaired sperm from old males. In guppies (*Poecilia reticulata*), *in vitro* fertilization assays have revealed that the ovarian fluid buffers the temporal decline in sperm quality that begins once sperm are released into the water (Gasparini & Evans, 2013). Whether such female adaptations have evolved to counteract the effect of mating with old males remains unknown, but this finding emphasizes the importance of considering male–female interactions when studying reproductive senescence.

The influence of paternal age on female reproductive senescence might be particularly important in species displaying assortative mating by age (i.e. when old females are paired with old males). For instance, any decrease in competitive abilities of old females could lead females to be less selective in mate choice and thereby to increase their probability of mating with old males, which increases the risk of sperm limitation or the risk of facing a lack of resources for offspring during the parental care period. Until now, age-assortative mating has mainly been documented in monogamous birds and seems to be rare in insects or mammals (Jiang, Bolnick & Kirkpatrick, 2013). In these latter classes, female preference for prime-age males, which has been documented in some species (Johnson & Gemmell, 2012), might have evolved in response to the poor quality of old male ejaculates (Beck & Promislow, 2007; Johnson & Gemmell, 2012). In addition, if females mating with old males are more likely to suffer from sperm limitation (i.e. when female fecundity is limited by the number of spermatozoa inseminated by one or more males), they might be more likely to initiate subsequent mating with potentially younger males (Radwan, 2003; Dean, Bonsall & Pizzari, 2007). Although a few studies in birds suggest that extra-pair copulations do not support such skewed age-distribution toward young males [e.g. reed bunting, *Emberiza schoeniculus* (Bouwman & Komdeur, 2005); bluethroat, *Luscinia svecica* (Laskemönen *et al.*, 2008)], how females adjust their remating rate according to the age of their partner remains poorly investigated. Such research is necessary for understanding how age-specific mate choice might have evolved according to the fertility costs described above or the potential genetic benefits of mating with old males (Manning, 1985; Brooks & Kemp, 2001).

Finally, male and female allocation to offspring can also interact after offspring birth and shape sex-specific patterns of reproductive senescence. Although paternal care is much less widespread than maternal care across animals (Kokko & Jennions, 2012), we cannot exclude that in species sharing parental care equally between sexes, such as many birds (Møller, 1988) or some mammals [e.g. savannah baboons, *Papio cynocephalus* (Buchan *et al.*, 2003)], a decline in the amount of paternal care with increasing age will impact female reproductive senescence (and *vice versa*) through an effect on offspring survival (Fay *et al.*, 2016; see also Fig. 1). Evidence that increasing age of fathers has strong deleterious effects on offspring health is accumulating (Zhu *et al.*, 2008), and epigenetic effects on male germ cells are often invoked as the underpinning biological cause. However, whether or not changes in paternal care with age are widespread in the wild remains to be assessed.

IV. THE ROLE OF TRADE-OFFS IN SHAPING REPRODUCTIVE SENESCENCE

As we emphasized above and in Fig. 1, reproduction is, in both sexes, a sequential process involving many physiological

and behavioural processes starting from gamete production and ending with the care provided to offspring. Here, we argue that future studies of reproductive senescence in the wild should not only consider the full set of traits influencing age-specific reproductive output but should also take into account the likely covariation in these traits. Below, we provide two examples of trade-offs in reproductive allocation, one in females (offspring size–number trade-off) and one in males (pre- and post-copulatory trade-off) and discuss their possible implications for the study of reproductive senescence.

(1) Offspring size–number trade-off

When females produce a single offspring per reproductive attempt, maximization of reproductive success can be reached by maximizing the probability of producing a viable offspring at each stage. However, in a large number of species, females produce several offspring per reproductive attempt. In this case, the simple maximization of reproductive success at each stage is prevented by an offspring size–number trade-off (Smith & Fretwell, 1974). Extra energy can be allocated either to one additional offspring without changing clutch or litter mass; to a higher average mass of the clutch or litter without changing the clutch or litter size; or to some compromise between these. This trade-off has led evolutionary ecologists to investigate the clutch or litter size that would maximise reproductive success, called optimal litter size (Lack, 1947) or Lack's clutch size (Godfray, Partridge & Harvey, 1991). Under the concept of individual optimization (Morris, 1985; Pettifor, Perrins & McCleery, 1988), the optimal clutch or litter size can [when each individual has its own optimal clutch or litter size (Murphy, 2000; Risch, Michener & Dobson, 2007)] or cannot [when all individuals have the same optimal clutch or litter size (Gaillard *et al.*, 2014)] vary among individuals within a population. In stark contrast to optimal clutch or litter size at the individual or population level that has received great attention, whether or not the optimal clutch or litter size should vary with age has been almost overlooked. Assuming that senescence will be associated with decreasing resource acquisition (e.g. through decreased food intake in relation to tooth wear in mammals or through impaired ability to convert food to energy), we should expect clutch/litter size or mass or both to decrease with increasing age (Begon & Parker, 1986). However, a given resource acquisition can lead to different optimal clutch or litter size depending on individual age, which leads to complex and barely predictable senescence patterns in clutch or litter mass and offspring size (Kindsvater *et al.*, 2010). In support of this prediction, the few empirical studies that have addressed age-specific variation in both clutch or litter size and offspring size displayed a large diversity of patterns (e.g. Ericsson *et al.*, 2001; Descamps *et al.*, 2008; Sharp & Clutton-Brock, 2010). To the best of our knowledge, only two studies have assessed the influence of maternal age on the offspring size–number trade-off, providing the same general outcome of no age-specific change in this trade-off. However, opposite senescence

patterns in offspring size and offspring number between the two focal species were hidden behind the pattern of a constant trade-off with age. In Soay sheep, old females trade offspring mass for litter size so that litter size remains constant with age but offspring mass declines with increasing age from 7 years onwards (Hayward *et al.*, 2013). By contrast, female Alpine marmots produce decreasing litter mass from 10 years of age onwards and trade litter size for offspring mass, causing litter size to decrease with increasing age while offspring mass does not change (Berger *et al.*, 2015b). Such contrasting offspring size–number trade-offs between Soay sheep and marmots likely evolved in response to marked differences in lifestyle and environmental conditions between these species. Environmental unpredictability might play a key role. In the highly stochastic environment of the Island of St Kilda (Northern Scotland), old female sheep maximise reproductive success through the number of offspring produced, whereas in the highly predictable environment offered by burrows in the French Alps, old female marmots maximise reproductive success through the quality of their offspring. To understand whether this represents a general pattern will require further theoretical and empirical studies.

(2) Pre- and post-copulatory trade-off

In many animal species, males have to face competition for mating (i.e. pre-copulatory competition) and for fertilizing eggs (i.e. post-copulatory competition) (Birkhead & Møller, 1998). As emphasized above, phenotypic adaptations for these two types of competition can show senescence (Table 1), implying that the success of males in both types is likely to decline with increasing age. However, an important consideration when studying male allocation to pre- and post-copulatory sexual traits is that males face a resource allocation trade-off between these two types of traits (Parker, Lessells & Simmons, 2012; Ferrandiz-Rovira *et al.*, 2014; Dines *et al.*, 2015) because both primary and secondary sexual traits are costly to produce and maintain (Dewsbury, 1982; Andersson, 1994; Thomsen *et al.*, 2006). Theoretical models have predicted that the quantity of expenditure in ejaculates should vary according to the mating role of the male (e.g. whether males mate in a favoured or non-favoured role; Parker, 1990) or their competitive environment (e.g. number of competitors per mating; Parker *et al.*, 2012), and empirical studies suggest that these trade-offs are widespread in a large range of species (e.g. Klaus *et al.*, 2011; Purnianmoorthy, Blanckenhorn & Schaffer, 2012; Dunn *et al.*, 2015). For example, in *Austropotamobius italicus*, a freshwater crayfish, there is a strong negative association between the size of the chelae (claws involved in antagonistic contests between males) and the size of the ejaculate (Galeotti *et al.*, 2012).

Although studies of covariation between pre- and post-copulatory traits are increasing, the effect of age on the intensity and shape of this trade-off has been neglected from both theoretical and empirical viewpoints. Generally, models that have been developed to investigate this question are based on the assumption that males have a total energy

budget for reproduction that they can share between pre- and post-copulatory competition. However, the quality and thus the efficiency of both primary and secondary sexual traits can decrease with increasing age (Table 1), possibly at different rates, and the marginal benefits of allocating preferentially to pre- or post-copulatory traits according to a given environmental condition (e.g. density of competitors in the population) might thus be age-dependent. To date, age-specific changes in the trade-off between pre- and post-copulatory traits have been investigated only in the domestic fowl, in a study that failed to detect age-specific covariation between comb size (pre-copulatory trait) and sperm quality (Cornwallis, Dean & Pizzari, 2014). In females, while a trade-off between comb size and gamete quality was absent in early life, negative covariation was detected at late ages, suggesting that decreasing somatic condition with increasing age might create the conditions for the evolution of trade-offs between sexual traits (Cornwallis *et al.*, 2014). Overall, there is a need for research incorporating the complex relationships linking traits responding to different selection pressures (such as pre- or post-copulatory sexual selection), somatic condition and age, notably in the wild where resources are limited and the trade-offs expected to be more acute. Such an approach would provide important insights into different reproductive and life-history strategies that have evolved to maximize fitness over the lifespan in the context of reproductive senescence.

V. THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON MALE AND FEMALE REPRODUCTIVE SENESCENCE

Variation in environmental conditions is now recognized as a key factor influencing patterns of actuarial senescence (Austad, 1993; Lemaître *et al.*, 2013; Holand *et al.*, 2016). However, the effects of environmental variation on reproductive senescence have been little studied even though their fitness consequences need to be quantified to assess accurately the demographic consequences of harsh environmental conditions, especially in the current context of climate change. Some studies have recently targeted the effect of environmental conditions on reproductive senescence. All these studies focused on the role of environmental conditions during early life [see Nussey *et al.* (2007) for a case study in mammals, and Bouwhuis *et al.* (2010); Cartwright *et al.* (2014) and Balbontín & Møller (2015) for case studies in birds], probably because under current theories of life-history evolution, early life stages are the most critical periods when available resources must be partitioned between growth, first reproductive events, and somatic maintenance (Lemaître *et al.*, 2015). In red deer, females born at high population density show accelerated reproductive senescence (Nussey *et al.*, 2007) and immigrant female great tits have higher rates of reproductive senescence than resident females, likely because these individuals initially suffered from a poor-quality natal environment (Bouwhuis *et al.*, 2010). If

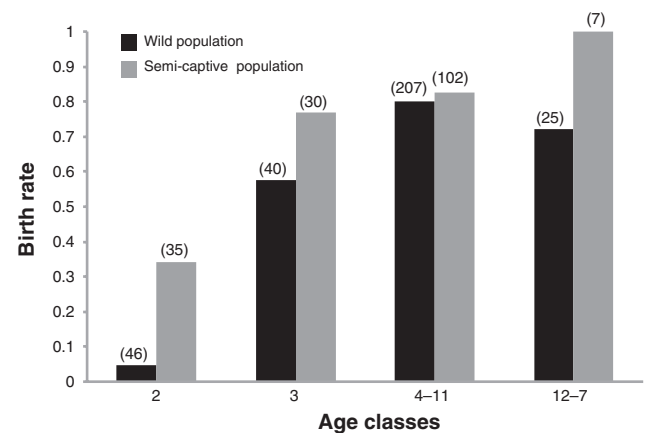


Fig. 3. Birth rates for wild (black) and semi-captive (grey) populations of ring-tailed lemurs (*Lemur catta*). Females from the wild population were studied in Berenty Reserve, southern Madagascar (Ichino *et al.*, 2015) and individuals from the semi-captive population were monitored on St. Catherine Island, Georgia, USA (Parga & Lessnau, 2005). Sample sizes for each age-class are provided in parentheses. When comparing birth rates between semi-captive and wild populations, no statistical difference occurs for prime-age (between 4 and 11 years old, z score test: $z = 0.53$, $P = 0.59$) but a statistically significant difference occurs for individuals older than 11 years old (z score test: $z = 3.08$, $P < 0.001$).

these studies indeed reveal that environmental conditions influence reproductive senescence, it is now pertinent to investigate the complexity of this relationship. Below, we list four important avenues that should help with this aim.

First, to evaluate the role of environmental conditions on life-history traits, captive (i.e. resources are generally provided *ad libitum*) and wild (i.e. resource availability is environmentally determined) populations can be compared. To date, the few published comparisons have focused on survival and actuarial senescence patterns (e.g. Bronikowski *et al.*, 2002; Clubb *et al.*, 2008; Lemaître *et al.*, 2013). Captive mammals show both a lower rate and later onset of senescence than their wild counterparts, an effect particularly pronounced in short-lived species (Tidière *et al.*, 2016). In zoological gardens, reproduction is sometimes controlled (e.g. Rhyen, Miller & Fagerstone, 2013), but when individuals are able to reproduce freely, captivity offers a unique opportunity to assess reproductive senescence in both sexes and for different reproductive traits when resources are abundant. Comparing the rate of reproductive senescence between captive and wild populations would shed new light on how environmental conditions mitigate reproductive senescence. Comparing birth rates between wild and semi-captive (provisioned with food and shelters) populations of ring-tailed lemurs (*Lemur catta*) suggests that increased resource availability might potentially protect against reproductive senescence. Although birth rates are consistently higher in the semi-captive population, the magnitude of the difference between the two environmental conditions reaches its maximum at old ages (Fig. 3).

Second, although most published studies focus on the influence of the natal environment on reproductive senescence, we should attempt to disentangle the roles of natal *versus* current conditions on the age-dependent pattern of reproductive performance. In Alpine marmots, early and adult social environments have independent and sometimes different effects depending on the life-history trait of interest (Berger *et al.*, 2015a). Interactive effects between early and adult environments have also been reported in the context of actuarial senescence in two ectothermic species, the yellow-legged frog (*Rana sierrae*) and the long-lived garter snake (*Thamnophis elegans*) (Miller *et al.*, 2014). In the context of reproductive senescence, the role of the current environment may be particularly important if a lack of resources reinforces the detrimental effects of old maternal age (van den Heuvel *et al.*, 2016). To date, the few studies of the effects of environmental conditions during adult life on age-specific changes in reproductive performance at the population level indicate more intense senescence in clutch size, egg volume and hatching success under high food availability, likely because middle-aged individuals benefit much more from favourable conditions than do young or old individuals [e.g. Oro *et al.* (2014) on Audouin's gull *Larus audouinii*].

Third, we urge researchers to investigate the impact of the environment on senescence in both sexes. In males, such studies should provide an explanation for the striking observation that similar secondary sexual traits evolved in closely related species often show distinct patterns of senescence. For instance, in some cervids antler size decreases at old ages [e.g. Vanpé *et al.* (2007) on roe deer, *Capreolus capreolus*], whereas it does not in others [e.g. red deer (Nussey *et al.*, 2009; Lemaître *et al.*, 2014)]. Moreover, senescence of antler size within a species can occur in some populations (Mysterud *et al.*, 2005) but not in others (Nussey *et al.*, 2009). This strongly suggests that the interaction between ecological conditions and life histories shapes both the occurrence and intensity of senescence in secondary sexual traits. There is now good evidence that environmental variation can have sex-specific effects on lifespan and actuarial senescence (e.g. birds: Wilkin & Sheldon, 2009; mammals: Garratt *et al.*, 2015), and we expect a similar situation for reproductive senescence. Assessing whether environmental conditions have sex-specific effects on reproductive senescence is of primary importance to understanding the interplay between male and female reproductive senescence.

Fourth, in the absence of a formal dedicated theoretical framework, reproductive senescence is often grounded in theories designed to explain the evolution of actuarial senescence, such as the antagonistic pleiotropy theory of ageing or the disposable soma theory (Lemaître *et al.*, 2015). Individuals that allocate extensively to reproduction early in life are thus predicted to suffer from earlier or faster reproductive senescence (Nussey *et al.*, 2006; Reed *et al.*, 2008; Bouwhuis *et al.*, 2010; Massot *et al.*, 2011; Lemaître *et al.*, 2014). However, although both processes are underpinned by

somatic deterioration, whether long-term reproductive costs should be expressed primarily in terms of reproductive or actuarial senescence has not been considered, and how such interplay might be influenced by environmental conditions remains unknown.

VI. CONCLUSIONS

(1) Although empirical evidence of reproductive senescence in the wild is now compelling, the study of this biological process is still in its infancy and requires a more comprehensive approach.

(2) Extending current research to all aspects of the female reproductive cycle (e.g. oocyte production, maternal care) and devoting efforts to the study of male reproductive senescence (e.g. in pre- and post-copulatory traits) should help to decipher the complexity of the interplay among factors shaping individual fitness in free-ranging populations.

(3) We demonstrate the importance of considering trade-offs in the study of reproductive senescence. For instance, incorporating offspring size–number trade-offs in females or pre- and post-copulatory trade-offs in males into studies of reproductive senescence allow us to understand the diversity of age-specific reproductive trajectories observed at the intra- and inter-specific levels.

(4) Assessing the influence of environmental conditions over the entire lifespan on reproductive senescence in both sexes should provide important insights into the dynamics of this process. Such studies are currently providing important results in the field of actuarial senescence and should be particularly important with regard to reproductive senescence.

(5) We highlight that such investigations should create exciting bridges between the ecology of senescence and areas of research in evolutionary ecology such as the study of mate choice, sperm competition and environmental stochasticity.

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