

Reproductive delays in mammals: an unexplored avenue for post-copulatory sexual selection

Teri J. Orr^{1,*},† and Marlene Zuk²

¹*Department of Biology, University of California, Riverside, CA 92521, U.S.A.*

²*Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, MN 55108, U.S.A.*

ABSTRACT

Numerous mammalian taxa exhibit reproductive delays, pauses in reproduction that occur between mating and fertilization, between fertilization and implantation of the embryo, or after an embryo has implanted. Of the 27 mammalian orders, 9 are known to exhibit reproductive delays, including Diptrotodontia, Dasyuromorphia, Eulipotyphya, Cingulata, Carnivora, Rodentia, Chiroptera, Lagomorpha and Cetartiodactyla. Most researchers interested in delays have focused on their evolutionary origins. However, the consequences of these delays have not been considered fully. Given the lengthening of the period over which reproduction occurs, it is possible that this unique aspect of reproduction facilitates post-copulatory sexual selection. When considered in the context of sexual selection, delays may allow sperm competition and female manipulation of fertilization (cryptic female choice) as well as other post-copulatory processes. We investigate the potential for reproductive delays to facilitate post-copulatory sexual selection and suggest avenues for research that may further our knowledge of sexual selection. We also provide a general review of reproductive delays in mammals.

Key words: Carnivora, chiroptera, cryptic female choice, delayed fertilization, delayed implantation, embryonic diapause, mammalia, post-copulatory sexual selection, reproductive delays, sperm competition.

CONTENTS

I. Introduction	2
II. The distribution of reproductive delays	3
III. Species with facultative delays	3
IV. The evolution of delays	6
V. Sexual selection and delays	8
(1) Delays between copulation and fertilization	9
(a) Predictions and experiments: delayed fertilization	10
(2) Delays between fertilization and implantation	14
(a) Cryptic female choice via selective implantation, zygote comparison, and re-absorption	14
(b) Predictions and experiments: delayed implantation	14
(3) Delays between implantation and birth (delayed development)	14
(a) Predictions and experiments: delayed development	14
VI. Additional consequences of delays	17
(1) Life history consequences of delays	17
(2) Post-copulatory sexual selection and the evolution of delays	18
(a) Predictions and experiments: post-copulatory sexual selection and the potential evolution of delays	18
VII. Conclusions	19
VIII. Acknowledgements	19
IX. References	19

* Author for correspondence (Tel: 951-723-7647; E-mail: tjorr@cns.umass.edu).

† Present address: Departments of Psychology and Biology, University of Massachusetts, Amherst, MA 01003, U.S.A.

I. INTRODUCTION

The study of vertebrate reproductive patterns has been of interest to biologists for centuries. Historically, researchers have approached the investigation of reproduction from an anthropocentric point of view, whereby they assumed the timing of events from fertilization to birth occurred in the same manner as in humans. Despite this common assumption, the diversity of mammalian reproductive physiology has also been recognized for some time (Hamlett, 1935). Indeed, even before the publication of Darwin's *On the origin of species by means of natural selection* in 1859, an unusual reproductive physiology, reproductive delays, had already been observed in mammals (Ziegler, 1843).

Extended periods of inactivity during a reproductive event are not restricted to mammals. Other animals and even plants are known to experience periods of reproductive diapause between fertilization and offspring sprouting/hatching or birth. For example, plants may have seeds that remain dormant (Bewley, 1997), female insects often store sperm (Pitnick, Markow & Spicer, 1999), and birds lay clutches of eggs asynchronously that often hatch synchronously, so that a given egg may undergo a delay in development (Ewert, 1992). Delays are less common in viviparous animals. However, in addition to mammals, some viviparous lizards (e.g. *Sceloporus jarrovi*) exhibit slow embryonic development similar to the reproductive delays of some mammals (Ballinger, 1979). The first documentation of this type of physiology in mammals was of the roe deer (*Capreolus capreolus*) which were known in 1843 to delay implantation for 4–5 months after fertilization (Hayssen, van Tienhoven & van Tienhoven, 1993). Similar types of delays in fertilization, implantation or development have since been described in many additional species of mammals. Well over 100 mammalian species, including members of the Diprotodontia, Dasyuromorphia, Eulipotyphya, Cingulata, Carnivora, Rodentia, Chiroptera, Lagomorpha and Cetartiodactyla have some form of reproductive delay (Hamlett, 1935; Mead, 1993), and this type of reproductive physiology may be even more widespread but still undocumented in additional species. Delaying fertilization, implantation, or pausing development (delayed development) may in turn alter the timing of subsequent events including parturition. For example, in the long-tailed weasel (*Mustela frenata*), implantation is delayed for 7–9 months while active gestation lasts an additional 9.5 months (Wright, 1942, 1963). The California leaf-nosed bat (*Macrotus californicus*) has delayed development for an average of 4.5 months, with active gestation lasting an additional 4 months (Bleier, 1975). Delayed fertilization is seen in the little brown bat (*Myotis lucifugus*), where females mate with males but store the sperm to be used at a later time. Thus, instead of fertilization occurring within a few days of mating, it occurs months later (Racey, 1982).

What is responsible for this diversity in reproductive timing? Several studies have examined the selective forces involved in the evolutionary origin of delays (Mead, 1989; Bernard & Cumming, 1997; Thom, Johnson &

Macdonald, 2004), which has led to some understanding of the advantages of delays (see Section IV below) and their taxonomic distribution (Mead, 1993). However, the consequences of such delays, once they have evolved, remain to be explored fully. Because reproductive delays lengthen the duration of a reproductive event from copulation to birth, they may provide additional time for post-copulatory sexual selection to operate (Table 1). For example, delayed fertilization increases the time frame during which sperm and ejaculates from various males might interact (sperm competition; Parker, 1970; Birkhead & Møller, 1993) or when females could manipulate and select sperm (cryptic female choice; Thornhill, 1983; Eberhard, 1996). During delayed implantation, post-copulatory processes could select among zygotes, allowing some to implant and others to be rejected. Finally, delayed development extends the period of time over which an embryo is in the female's reproductive tract (Bernard & Cumming, 1997), potentially facilitating its re-absorption or rejection (abortion).

In this review we first describe the distribution of reproductive delays among mammals, briefly review the literature on the evolution of delays and define the types of reproductive delays. Delays are then discussed in greater detail in the order in which they might occur in a typical pregnancy: delayed fertilization, implantation and then development. For each type of delay we ask what modes of sexual selection might be operating. After evaluating the likelihood of sexual selection during each delay type (and corresponding time frame) we suggest experiments to test the hypothesis that delays facilitate post-copulatory sexual selection, and offer potential avenues for future research. Finally, for each delay type, we review the data consistent with these expectations (Table 2). Although we focus here on mammals, the predictions outlined in this review would be relevant to any animal or plant with delay-like reproductive asynchrony.

The existence of reproductive delays presents an ideal opportunity for asking questions about female *versus* male control of reproduction. Because specific stages of reproduction are lengthened in species with delays, these stages can be scrutinized for what may be evidence of sexual selection. For example, fertilization may primarily serve as an arena for male competitive strategies, while delayed development may provide opportunities for females to manipulate events (and the embryos themselves), and implantation might be a period of extreme sexual conflict. We believe delays are an under-appreciated source of natural variation in reproductive physiology, the investigation of which could allow important insights into cryptic female choice or sperm competition. Birkhead & Møller (1993) discussed the possible role of sperm storage (delayed fertilization) in facilitating sperm competition. However, the idea that delays at other points during the reproductive cycle might be important in post-copulatory sexual selection (Table 1) has remained largely ignored for the last 20 years subsequent to Birkhead & Møller's (1993) paper. Meanwhile, our knowledge of post-copulatory

Table 1. Definitions of terms associated with reproductive delays and modes of sexual selection

Term	Definition
Active gestation	Period of development from egg fertilization until birth that does not include the duration of delays.
Cryptic female choice	Ability of polyandrous females to bias paternity after copulation, termed 'cryptic' because it is not easily observed in the confines of the reproductive tract (Thornhill, 1983).
Delayed fertilization	Extension of time between copulation and actual use of sperm to fertilize eggs; due to sperm storage and/or delayed ovulation (Vaughan, Ryan & Czaplewski, 2000).
Delayed implantation	Period of delay occurring after a blastocyst has formed, when cell division stops and the blastocyst remains unattached for a prolonged period of time; also called 'embryonic diapause' (Daniel, 1970).
Delayed development	Period of suspended or slow growth of the embryo that can occur after implantation has occurred but prior to birth (Bernard & Cumming, 1997).
Delayed ovulation	A type of delayed fertilization whereby ovulation is delayed, resulting in fertilization also being delayed (Hamlett, 1935).
Facultative delays	Delays that depend on environmental or female conditions such as low food availability or females nursing other young while pregnant (Daniel, 1970; Mead, 1993).
Genetic inviability avoidance	Selection for or against certain genetic combinations after fertilization and subsequent recombination of the maternal and paternal genetic information has occurred; potentially used to avoid the costs and risks associated with prolonged investment in incompatible (poor) offspring genotypes (Zeh & Zeh, 1996, 1997).
Pre-copulatory sexual selection	Individual variation in relative ability to gain matings that result in successful fertilizations (Eberhard, 1996).
Post-copulatory sexual selection	Sexual selection occurring after mating whereby individuals vary in their relative ability to gain fertilizations (Eberhard, 1996).
Reproductive diapause/delays	Deviation from continuous development in mammalian reproduction, with periods of dormancy in the egg, blastocyst or embryo (Vaughan <i>et al.</i> , 2000).
Sexual conflict	Pay-offs of a certain event (usually fertilization) deviate drastically between males and females resulting in a competing arms race between the sexes with each sex pushing for control over fertilization (Arnqvist & Rowe, 2005).
Sperm competition	Contest for successful fertilization of an ovum within a single female between sperm from more than one male (Parker, 1970). This definition has been expanded and includes substances in the ejaculates of males that might play a role in paternity-biasing processes (Montoto <i>et al.</i> , 2011).
Sperm storage (female)	Maintenance of sperm in a female's reproductive tract for extended periods of time, requiring special structures in some animals (Fenton, 1984). We refine this definition to include only cases where sperm are contained in the female's tract for a period of time longer than usual sperm longevity.

sexual selection, reproductive physiology (Heideman & Powell, 1998; Krishna, 1999; Oates *et al.*, 2007), and the evolutionary relationships of mammals (Wilson & Reeder, 2005; Bininda-Emonds *et al.*, 2007; Miller-Butterworth *et al.*, 2007; Meredith *et al.*, 2011; Nyakatura & Bininda-Emonds, 2012) have grown substantially.

II. THE DISTRIBUTION OF REPRODUCTIVE DELAYS

Over 100 mammalian species exhibit some type of reproductive delay (Hayssen *et al.*, 1993; Mead, 1993). The distribution of reproductive delays among mammals is complex. For example, delays are found in the infraclass Metatheria (Marsupials) while bats as a more derived order appear to exhibit multiple origins of all three types of delays (delayed fertilization, implantation, development) (Mead, 1993). In other groups, delays might have been the ancestral state lost in recent species as suggested for the Carnivora (Lindenfors, Dalen & Angerbjörn, 2003). Of the 27 recognized mammalian orders (Wilson & Reeder, 2005), 9 are known to have some type of reproductive delay

(Table 3). The best studied group with reproductive delays is the Carnivora, with 68 species known to have delayed implantation, 132 known to not delay implantation and a remaining 71 species for which data are unavailable (Orr, 2012). Thus, the Carnivora are a good study group given the prevalence of data both on absence and presence of delays. Another group, the bats (order Chiroptera), are also valuable in the context of delays because they possess all three types of reproductive delay: delayed fertilization, implantation and development (Oxberry, 1979; Racey, 1982; Bernard & Cumming, 1997). For these reasons our review focuses on two taxonomic groups: the Carnivora and Chiroptera.

III. SPECIES WITH FACULTATIVE DELAYS

Some mammalian species have delays that only occur under certain environmental conditions, termed facultative delays. Conditions that may induce facultative delays include changes in photoperiod (Temte, 1985), food deprivation (Rasweiler & Badwaik, 1997), concurrent lactation (Weichert, 1940; Renfree, 1979) or variation in ambient temperatures (Uchida, Inoue & Kimura, 1984).

Table 2. Evidence suggestive of post-copulatory sexual selection occurring during the reproductive cycle of various species with reproductive delays

Phenomena consistent with sexual selection	Order	Species	Common name	Delay type	Source
Large percentage of multiple paternity within a single litter	Artiodactyla	<i>Capreolus capreolus</i> (15.5% multiple paternity)	Roe deer	Delayed implantation	Review: Soulsbury (2010)
	Chiroptera	<i>Eptesicus fuscus</i> (46.2% multiple paternity)	Big brown bat	Delayed development	Vonhof <i>et al.</i> (2006); review: Soulsbury (2010)
	Chiroptera	<i>Lasiurus borealis</i> (20.0% multiple paternity)	Eastern red bat	Delayed fertilization	Review: Soulsbury (2010)
	Chiroptera	<i>Pteropus alecto</i> , <i>P. conspicillatus</i> , <i>P. poliocephalus</i>	Flying foxes	—	Fox <i>et al.</i> (2008)
	Rodentia	<i>Mus musculus</i> (5.6–42.9% multiple paternity)	House mouse	Facultative delayed implantation	Review: Soulsbury (2010)
	Lagomorpha	<i>Lepus americanus</i> (25.0% multiple paternity)	Snowshoe hare	*Other taxa in same genus have delays	Review: Soulsbury (2010)
	Carnivora	<i>Gulo gulo</i> (12.5% multiple paternity)	Wolverine	Delayed implantation	Review: Soulsbury (2010)
	Carnivora	<i>Haliastur gyrfalco</i>	Grey seal	Delayed implantation	Review: Birkhead & Appleton (1998)
	Carnivora	<i>Meles meles</i> (16.1–44.8% multiple paternity)	European badger	Delayed implantation	Review: Soulsbury (2010)
	Carnivora	<i>Mustela erminea</i> (16.7% multiple paternity)	Short-tailed weasel, ermine	Delayed implantation	Holland & Gleeson (2005) Review: Soulsbury (2010)
	Carnivora	<i>Mustela (Neovison) vison</i> (33.3% multiple paternity)	American mink	Delayed implantation	Yamaguchi <i>et al.</i> (2004) Review: Soulsbury (2010)
	Carnivora	<i>Ursus americanus</i> (20.0–50.0% multiple paternity)	American black bear	Delayed implantation	Review: Soulsbury (2010)
	Polytocous with variable litter sizes (this trait is particularly noteworthy for bats which usually have litter sizes of $N = 1$ (Kurta & Kunz, 1987). Many species listed above would also fall into this section)	Carnivora	<i>Ursus arctos</i> (13.3–28.1% multiple paternity)	Brown (grizzly) bear	Delayed implantation
Carnivora		multiple paternity <i>Vulpes vulpes</i> (37.5% multiple paternity)	Red fox	Facultative delayed implantation	Review: Soulsbury (2010)
Chiroptera		<i>Chalinolobus gouldii</i>	Gould's wattled bat	Delayed fertilization	Kitchner (1975)
Chiroptera		<i>Eptesicus fuscus</i>	Big brown bat	Delayed fertilization	Christian (1956) and Wimsatt (1942, 1945)
Chiroptera		<i>Lasiopycteris noctivagans</i>	Sliver-haired bat	Delayed implantation	Wimsatt (1945)
Chiroptera		<i>Lasiurus borealis</i>	Eastern red bat	Delayed fertilization	Allen (1939)
Chiroptera		<i>Myotis austroriparius</i>	Southeastern myotis	*	Sherman (1930) and Rice (1957)
Chiroptera		<i>Myotis lucifugus</i>	Little brown bat	Delayed fertilization	Guthrie (1933)
Chiroptera		<i>Parastrellus hesperus</i>	Western pipistrelle	Delayed fertilization	Kruttsch (1975)

Table 2. Continued

Phenomena consistent with sexual selection	Order	Species	Common name	Delay type	Source
	Chiroptera	<i>Perimyotis subflavus</i>	Eastern pipistrelle	Delayed fertilization	Guthrie (1933) and Wimsatt (1945)
	Chiroptera	<i>Scotophilus kuhlii</i>	Lesser Asiatic yellow house bat	*	Gopalakrishna (1949)
Abortion and re-absorption of embryos	Chiroptera	<i>Tylonycteris pachypus</i>	Lesser bamboo bat	Delayed fertilization	Medway (1972)
	Chiroptera	<i>Lasiurus borealis</i> , <i>L. cinereus</i> , <i>L. ega</i>	Tree bats (Eastern red bat, hoary bat, and southern yellow bat)	Delayed fertilization	Shump & Shump (1982a,b), Kurta & Lehr (1995) and Bouchard, Zigouris & Fenton (2001)
	Chiroptera	<i>Saccopteryx bilineata</i>	Greater sac-winged bat	Delayed development	Bradbury & Vehrencamp (1976, 1977)
	Rodentia	<i>Rattus norvegicus</i> , <i>Mus musculus</i>	Lab rat, house mouse	Facultative delayed implantation	Conoway (1955) and Lloyd & Christian (1969)
	Carnivora	<i>Lontra canadensis</i>	American river otter	Delayed implantation	Conoway (1955) and Lloyd & Christian (1969)
Ovulation during pregnancy (superfetation)	Diprotodontia	Macropodidae (various)	Kangaroos and wallabies	Delayed implantation	Tyndale-Biscoe & Renfree (1987)
	Chiroptera	<i>Carollia perspicillata</i>	Seba's short-tailed bat	Delayed development	Roellig <i>et al.</i> (2011)
	Chiroptera	<i>Rousettus leschenaultia</i>	Fulvous fruit bat	—	Roellig <i>et al.</i> (2011)
	Lagomorpha	<i>Lepus europaeus</i>	European hare	Delayed fertilization	Roellig <i>et al.</i> (2011)
	Carnivora	<i>Meles meles</i>	Eurasian badger	Delayed implantation	Roellig <i>et al.</i> (2011)
	Carnivora	<i>Mustela (Neovison) vison</i>	American mink	Delayed implantation	Roellig <i>et al.</i> (2011)
Reproductive tract distinguishes between eggs and moves them differentially within the female's tract suggesting female control	Chiroptera	<i>Glossophaga soricina</i>	Pallas' long-tongued bat	Delayed implantation	Rasweiler (1979) and Badwaik & Rasweiler (2000)
	Chiroptera	<i>Noctilio albiventris</i>	Lesser bulldog bat	Delayed fertilization	Rasweiler (1979) and Badwaik & Rasweiler (2000)
Paternity biases, same father across colony despite mating 'on-the-wing'	Chiroptera	<i>Peropteryx kappleri</i>	Greater dog-like bat	—	Rasweiler (1979) and Badwaik & Rasweiler (2000)
	Chiroptera	<i>Saccopteryx bilineata</i>	Greater sac-winged bat	Delayed development	Voigt, Heckel & Mayer (2005)
Multiple eggs ovulated (up to seven) but only one implants	Chiroptera	<i>Perimyotis subflavus</i>	Eastern pipistrelle	*	Wimsatt (1945)
	Chiroptera	<i>Myotis molaccarum</i>	Large-footed myotis	Delayed fertilization (short period)	Lloyd <i>et al.</i> (1999)
Selective implantation (multiple ovulation, only one fertilized)	Chiroptera	<i>Gynomops planirostris</i>	Southern dog-faced bat	—	Ryan (1991)
	Chiroptera	<i>Gynopterus sphinx</i>	Greater short-nosed bat	Facultative delayed development	Vambarkar (1958)
Penile elaborations (spines)	Chiroptera	<i>Lasiurus borealis</i> , <i>Lasiurus cinereus</i>	Tree bats	Delayed fertilization	P. M. Cryan, unpublished data
	Chiroptera	<i>Mormopterus jugularis</i> <i>Nyctinomops laticaudatus</i>	Peter's wrinkle-lipped bat Broad-eared bat	—	Ryan (1991) Ryan (1991)

Table 2. Continued

Phenomena consistent with sexual selection	Order	Species	Common name	Delay type	Source
	Chiroptera	<i>Pteropus giganteus</i>	Indian flying fox	—	Vamburkar (1958)
	Chiroptera	<i>Rhinonictes aurantius</i>	Orange horseshoe bat	*	Armstrong (2005)
	Chiroptera	<i>Tadarida brasiliensis</i>	Brazilian free-tailed bat	—	Ryan (1991)
Penile elaborations (scoops)	Chiroptera	<i>Cardioderma cor</i>	Heart-nosed bat	—	Matthews (1942)
	Chiroptera	<i>Tricainops afer</i>	Triple nose-leaf bat	—	Matthews (1942)
Buccular selection (increased size; authors also noted differences in complexity of shape but did not evaluate statistically)	Carnivora	<i>Pagophilus (Phoca) groenlandica</i>	Harp seal	Delayed implantation	Miller & Burton (2001)

If a closely related species has reproductive delays, an * indicates that the listed species may also have delays.

Dashes (—) indicate species for which delays are unknown, and it is unknown if related species have delays or not.

Facultative delays may occur during any of the three stages described above, but delayed fertilization and implantation appear to be the most common types of facultative delays (Table 4). Additionally, at least one species (red fox, *Vulpes vulpes*) is known to be polymorphic for delays, with delays only occurring in some parts of the species' range (Larivière & Pasitschniak-Arts, 1996). Species with facultative delays are particularly useful for addressing the questions outlined in this review, as they provide an opportunity to contrast circumstances that do and do not co-occur with delays in a single species.

IV. THE EVOLUTION OF DELAYS

While the aim of this review is to evaluate the consequences of delays once they have already evolved, information regarding their origins is informative. The origins of reproductive delays have been examined and reviewed by numerous authors (Hamlett, 1935; Sandell, 1990; Mead, 1993; Bernard & Cumming, 1997; Racey & Entwistle, 2000; Ferguson, Higdon & Larivière, 2006). Hamlett (1935) summarized several ideas regarding the origins of delays in mammals, including: (i) delays allow young to be born at an energetically favorable time; (ii) delays only occur in old genera that existed during the Pleistocene, because delays assured young were not born during glacial winters, and (iii) delays are a byproduct of lower body temperatures of hibernating mammals. Hamlett (1935) also suggested (iv) that delays are not adaptive, but instead are the ancestral state in some species.

Several additional hypotheses regarding the origin of reproductive delays, many expansions on Hamlett's (1935) ideas, have been published in the last 60 years. These fall roughly into Hamlett's four original categories. Consistent with Hamlett's first hypothesis, delays may allow females to match the energetic demands of pregnancy and lactation to food abundances and favourable weather (Ferguson *et al.*, 2006) or, more specifically, to wean young when food is available (van der Merwe, 1978). Similarly, females might use delays to ensure that oestrus coincides with periods of mate availability to elicit maximal male competition, thereby providing opportunity for female mate choice (Sandell, 1990). Delays likely enable the synchronization of seasonal breeding, as seen in marine mammals such as pinnipeds (Bartholomew, 1970). Indeed, because pinnipeds are widely dispersed much of the year, the selective advantage of being able to have parturition occurring in a narrow window during which mating also occurs (shortly thereafter) is important (Bartholomew, 1970). Synchronization may allow young to reach independence at roughly the same time and thus saturate predators and increase relative survival rates (Racey, 1982; Bernard & Cumming, 1997).

In regard to Hamlett's (1935) second hypothesis, delays may have been an ancestral state that was lost to counteract other changes in life histories associated with the evolution of decreased body mass (Ferguson, Virgl & Larivière, 1996; Lindenfors *et al.*, 2003). Because otherwise non-delaying

Table 3. Mammalian orders known to exhibit delays (underlined) listed with number of species known to have delays. Type of delays observed are listed; delayed fertilization, delayed implantation, and delayed development are given together with an estimated total number of species in each order and original citations if not cited in a later table

Order	Representative taxa	Species known to have delays	Species known to not delay	Number of species in Order	Delay type	Source
Subclass PROTOTHERIA						
Monotremata	Platypus, echidna	6	—	6	—	—
Infraclass METATHERIA						
Dasyuromorphia	Carnivorous marsupials	2	—	~71	Fertilization	Marlow (1961); also see Table 5
Didelphimorphia	Opossums	0	1: Virginia opossum (<i>Didelphis virginiana</i>)	> 60	—	Hartman (1923)
Diprotodontia	Kangaroos, wallabies, possums	~23	2: mountain pygmy-possum (<i>Burramys parvus</i>), common brush-tail possum (<i>Trichosurus vulpecula</i>)	~120	Implantation, (facultative in some species)	Gilmore (1969) and Renfree & Shaw (2000); also see Tables 4 and 7
Microbiotheria	Monito del monte	0	—	1	—	—
Notoryctemorphia	Marsupial moles	0	—	2	—	—
Paucituberculata	Shrew opossums	0	—	5	—	—
Peramelemorphia	Bandicoots, bilbies	0	1: long-nosed bandicoot (<i>Perameles nasuta</i>)	~19	—	Hughes (1962b)
Subclass THERIA						
Infraclass EUTHERIA						
Afrosoricida	Tenrecs, golden moles	0	—	~51	—	—
Carnivora	Lions, bears, seals	68	132	271	Implantation	Orr (2012); Table 7
Cetartiodactyla	Even-toed ungulates, dolphins, whales	~2	1: reindeer (<i>Rangifer tarandus</i>)	310	Implantation	Retzius (1900); also see Table 7
Chiroptera	Bats	> 100	—	> 1200	Fertilization, implantation, development	See Tables 4–8
Cingulata	Armadillos	2	—	20	Implantation	See Table 7
Dermoptera	Flying lemurs	0	—	2	—	—
Eulipotyphla	Shrews, moles	2	—	~359	Implantation	See Table 7
Hyracoida	Hyraxes	0	—	4	—	—
Lagomorpha	Rabbits, hares, pika	1	—	80	Fertilization	See Table 5
Macroscelidea	Elephant shrews	0	—	19	—	—
Perissodactyla	Odd-toed ungulates	0	—	~19	—	—
Pholidota	Pangolins	0	—	7	—	—
Ptilosa	Sloths, anteaters	0	—	10	—	—
Primates	Monkeys, apes	0	—	424	—	—
Proboscidea	Elephants	0	—	3	—	—
Rodentia	Rats, squirrels, mice	~9	—	2277	Implantation	Renfree & Calaby (1981)
Scandentia	Tree shrews	0	—	20	—	—
Sirenia	Manatees, dugongs	0	—	4	—	—
Tubulidentata	Aardvarks	0	—	1	—	—

Table 4. Species known to exhibit facultative reproductive delays listed with the presumed driver of the delay

Order	Family	Species	Common name	Delay type	Cause	Source
Diprotodontia						
	Macropodidae	<i>Macropus eugenii</i>	Tammar wallaby	Delayed implantation	Lactation	Berger (1966)
		<i>Setonix brachyurus</i>	Quokka	Delayed implantation	Lactation	Sharman (1955 <i>b</i>) and Shield (1968)
		<i>Macropus rufogriseus</i>	Red-necked wallaby	Delayed implantation	Lactation	Merchant & Calaby (1981) and Fleming, Cinderey & Hearn (1983)
		<i>Macropus rufus</i>	Red kangaroo	Delayed implantation	Lactation	Sharman & Pilton (1964) and Clark (1966)
Chiroptera						
	Emballonuridae	<i>Taphozous longimanus</i>	Long-winged tomb bat	Delayed development	Temperature	Krishna & Dominic (1982)
	Pteropodidae	<i>Ptenochirus jagori</i>	Greater fruit musky bat	Delayed development	Maternal age	Heideman & Powell (1998)
		<i>Cynopterus sphinx</i>	Greater short-nosed bat	Delayed development (gastrulation)	Fat stores	Meenakumari & Krishna (2005)
	Vespertilionidae	<i>Miniopterus schreibersii</i>	Schreiber's long-fingered bat	Delayed implantation	Temperature	Baker & Bird (1936)
Rodentia						
	Muridae	<i>Dipodillus simoni</i>	Simon's dipodil	Delayed implantation	Lactation	Hamlett (1935)
		<i>Meriones longifrons</i>	Mongolian gerbil	Delayed implantation	Lactation	Hamlett (1935)
		<i>Meriones shawi</i>	Shaw's jird	Delayed implantation	Lactation	Hamlett (1935)
		<i>Mus musculus</i>	House mouse	Delayed implantation	Lactation	McLaren (1968)
		<i>Rattus norvegicus albinus</i>	White lab rat	Delayed implantation	Lactation	King (1913)
Carnivora						
	Canidae	<i>Vulpes vulpes</i>	Red fox	Delayed implantation	Polymorphic across range	Larivière & Pasitschniak-Arts (1996)

species such as domestic sheep (*Ovis aries*) can be forced to undergo reproductive delays, Ptak *et al.* (2012) argued that delays must be conserved across mammals and thus secondarily lost. Hamlett's third hypothesis, that lowered body temperatures cause delays, is no longer widely accepted because many taxa that have delays live in tropical or very warm habitats (e.g. *Artibeus jamaicensis*: Fleming, 1971; *Macroglossus minimus*: Hood & Smith, 1989; and *Carollia perspicillata*: Rasweiler & Badwaik, 1997; see also Bernard & Cumming, 1997; Racey & Entwistle, 2000). However, consistent with Hamlett's fourth hypothesis, it has been suggested that delays might be a genetic byproduct of changes to other aspects of reproductive physiology (Isakova, 2006). The most commonly accepted view is that delays enable females to negotiate seasonal environments and in so doing reap energetic, nutritional or mate-choice benefits (Fleming, 1971; Bernard & Cumming, 1997; Ferguson *et al.*, 2006).

An additional hypothesis regarding the origins of reproductive delays includes a function in sexual selection. It has been suggested that delays allow for mate choice in cases where there is a lack of home range overlap during parts of the year (Ferguson *et al.*, 2006). If delays were simultaneously under both natural and sexual selection, to evaluate the importance of each type of selection one could

evaluate natural history correlates (ecology and body size, for example) as compared to those consistent with sexual selection (mating system, testes, sperm traits). For example, pairs of delaying species with matched ecologies but different mating systems or *vice versa* might be compared. Traits may be said to result from sexual selection if closely related species without delays but with the same ecology/mating system do not share the trait under question. Species that facultatively delay and or are polymorphic for delays could be utilized to determine if any of the hypothesized selective advantages of delays are associated with the presence or absence of delays.

V. SEXUAL SELECTION AND DELAYS

Regardless of their evolutionary origin, once they are present, delays can provide an extended opportunity for sexual selection to act after copulation. Sexual selection has long been known to occur prior to copulation, but it has been shown also to operate *via* post-copulatory sexual selection, which as the name suggests is sexual selection that occurs after mating. Post-copulatory sexual selection is frequently divided into two categories: sperm competition (the rivalry between sperm and/or ejaculates from different males for

the fertilization of an egg) and cryptic female choice (biases in paternity due to female-driven processes after mating) (Parker, 1970; Thornhill, 1983; Table 1). Reproductive delays are likely to facilitate both processes.

Outlined below are the different delay types as they occur sequentially in a typical pregnancy. We focus our review on delayed fertilization and to a lesser degree delayed implantation with some mention of delayed development. This bias is representative of the number of species known to have these delays as well as the recognized types of post-copulatory sexual selection, most of which occur prior to or during fertilization as opposed to between fertilization and implantation or after implantation. Thus the potential for post-copulatory sexual selection may be greater during delayed fertilization than during delayed implantation (and delayed development). In some situations, expectations for both male- and female-based post-copulatory sexual selection will be identical or barely distinguishable.

(1) Delays between copulation and fertilization

After mating, a delay of variable length may occur between insemination and fertilization (Table 5). Termed delayed fertilization, this phenomenon occurs when females store sperm. In most cases, they also delay ovulation for up to an entire season (Wimsatt, 1979). Most female mammals, unlike insects, birds, or squamates, generally do not store sperm for long periods of time, with the exception of some bats (Racey, 1979; Birkhead, 2000). In addition to sperm storage being relatively uncommon in mammals, they also generally lack special sperm storage structures like the spermathecae of insects, or sperm-storage tubules of birds (Birkhead, 2000; Orr & Zuk, 2012). However, some mammals co-opt pre-existing structures, namely the lining of the reproductive tract, to store sperm (Racey & Potts, 1970; Racey, 1979; Table 5). Why mammals lack highly specialized sperm-storage structures, how they are able to store sperm and when the evolutionary transition to the mammalian short sperm

Table 5. Species known to exhibit delayed fertilization (sperm storage, delayed ovulation)

Order	Family	Species	Common name	Delay length (days)	Source
Carnivora	Canidae	<i>Canis familiaris</i>	Domestic dog	11	Birkhead & Møller (1993)
Chiroptera	Molossidae	<i>Molossus ater</i>	Black mastiff bat	50	Rasweiler (1987)
	Noctilionidae	<i>Noctilio albiventris</i>	Lesser bulldog bat	—	Rasweiler (1977)
	Pteropodidae	<i>Macroglossus minimus</i> •	Long-tongued bat	60–90	Hood & Smith (1989)
				*implicated	
	Rhinolophidae	<i>Rhinolophus ferrumequinum</i>	Greater horseshoe bat	150	Matthews (1937) and Racey (1975)
	Vespertilionidae	<i>Chalinolobus gouldii</i>	Gould's wattled bat	—	Kitchner (1975)
		<i>Eptesicus furinalis</i>	Argentine brown bat	—	Myers (1977)
		<i>Eptesicus fuscus</i>	Big brown bat	156	Gates (1936) and Wimsatt (1944)
		<i>Lasiurus borealis</i>	Eastern red bat	—	P. M. Cryan, unpublished data
		<i>Lasiurus cinereus</i>	Hoary bat	—	P. M. Cryan, unpublished data
		<i>Lasiurus ega</i>	Southern yellow bat	—	Myers (1977)
		<i>Myotis dasycneme</i>	pond myotis	—	Strelkov (1962)
		<i>Myotis daubentonii</i>	Daubenton's bat	—	Strelkov (1962)
		<i>Myotis lucifugus</i>	Little brown bat	~100	Wimsatt (1944)
		<i>Myotis mystacinus</i>	Whiskered bat	—	Strelkov (1962)
		<i>Myotis ricketti</i>	Rickett's big-footed bat	225	Wang <i>et al.</i> (2008)
		<i>Myotis sodalis</i>	Indiana bat	68	Gates (1936)
		<i>Myotis velifer</i>	Cave myotis	—	Krutzsch <i>et al.</i> (1982)
		<i>Nyctalus noctula</i>	Common noctule	198	Racey (1973a,b)
		<i>Nyctophilus geoffroyi</i>	Lesser long-eared bat	~90	Hosken (1998)
		<i>Perimyotis subflavus</i>	Eastern pipistrelle	—	Guthrie (1933)
		<i>Pipistrellus abramus</i>	Japanese house bat	175	Hiraiwa & Uchida (1956)
		<i>Pipistrellus ceylonicus</i>	Kelaart's pipistrelle	30	Racey (1979)
		<i>Pipistrellus nanus</i>	Banana pipistrelle	75	Bernard & Cumming (1997)
		<i>Pipistrellus pipistrellus</i>	Common pipistrelle	151	Pagenstecher (1859) and Racey (1973b)
		<i>Plecotus auritus</i>	Brown long-eared bat	—	Strelkov (1962)
		<i>Scotophilus heathi</i>	Greater Asiatic yellow bat	60	Krishna & Dominic (1982)
		<i>Tylonycteris pachypus</i>	Lesser bamboo bat	< 30	Medway (1972)
		<i>Tylonycteris robustula</i>	Greater bamboo bat	< 30	Medway (1972)
Dasyuromorphia	Dasyuridae	<i>Antechinus stuartii</i>	Brown antechinus	16	Birkhead & Møller (1993)
		<i>Dasyurus viverrinus</i>	Eastern quoll	14	Birkhead & Møller (1993)
Lagomorpha	Leporidae	<i>Lepus europaeus</i>	European hare	30	Birkhead & Møller (1993)

Dashes indicate that the length of the delay is unclear. •This species (*Macroglossus minimus*) has been subject of debate (see Racey & Entwistle, 2000) and should be carefully evaluated for correct assignment of delay type.

life cycle occurred remain interesting questions worthy of further inquiry (see Holt, 2011).

Delayed fertilization can offer an opportunity for cryptic female choice when little opportunity exists for pre-copulatory mate selection. For example, females of many temperate bat species such as *Myotis lucifugus* (Thomas, Fenton & Barclay, 1979; Wai-Ping & Fenton, 1988), *Nyctalus nyctula* (Racey, 1973a) and *Corynorhinus townsendii* (Pearson, Koford & Pearson, 1952) are mated by males while in torpor. Cryptic female choice may give them their only opportunity for exerting mate choice. Similarly, mating occurs 'on the wing' in some species (e.g. *Lasiurus borealis*, Murphy & Nichols, 1913), possibly limiting female pre-copulatory mate assessment. Some of these species are temperate bats that have minimal pre-copulatory sexual selection opportunities because males and females migrate separately (Wai-Ping & Fenton, 1988). Could the details of mate choice be worked out in the confines of the female's reproductive tract in species with delayed fertilization? Most bats only have one or two young per litter (Kurta & Kunz, 1987) so females probably receive enough sperm from a single copulation for successful fertilization. For this reason, the potential for post-copulatory sexual selection in these taxa seems particularly worthy of investigation. Delayed fertilization could facilitate three forms of post-copulatory sexual selection: sperm competition, cryptic female choice (including female sperm selection and selective ovulation), and genetic incompatibility avoidance.

The lengthened period of female receptivity to sperm due to delayed fertilization greatly increases the opportunity for remating and thus sperm co-occurrence and as a result sperm competition. If females store sperm from several males, Parker's (1970) requisites for sperm competition are satisfied; namely, the co-occurrence of sperm from more than one male inside the female's reproductive tract. Indeed, females of many species with delayed fertilization mate multiple times (Miller & Burton, 2001; Vonhof *et al.*, 2006; Table 2).

Where might we look for evidence of sperm competition? Morphological indications of sperm competition may be noted in both reproductive anatomy and sperm cell morphology (Gage, 1998; Pitnick, Hosken & Birkhead, 2009) including relatively larger testes (e.g., Harcourt *et al.*, 1981), elaboration in female internal reproductive morphology (Eberhard, 1996; Brennan *et al.*, 2007), and penile (bone or cartilaginous) structures (Eberhard, 1985; Dixson, 1987; Hogg, 1988; Edwards, 1993). Furthermore, sperm performance itself (e.g. swimming speed) may be altered in the context of sperm competition and may in some cases evolve independently of sperm length or other morphological variables (Kleven *et al.*, 2009).

Demonstrating that sperm from several males co-occur within the female's reproductive tract would be important primary evidence of sperm competition risk. A better indication of sperm competition would involve highly controlled mating trials followed by paternity analyses (for example, see Evans, Pierotti & Pilastro, 2003) and examination of sperm or ejaculate characteristics as they

relate to successful fertilization. The possible evidence for sperm competition is discussed in more detail below.

(a) *Predictions and experiments: delayed fertilization*

Below we make predictions about the opportunities for post-copulatory sexual selection in species with delayed fertilization. Male interests may be subverted by females during delays. As a result, delays may present an increased opportunity for sexual conflict (see Prediction 11 in Section VI.2a). We also suggest experiments or other work that could be used to test these predictions.

Prediction 1: Species with delayed fertilization are expected to have sperm traits that facilitate their competitive abilities, such as increased sperm longevity or binding affinities. Species with delays are expected to have unique or exaggerated sperm features such as larger mid-pieces, and additional mitochondria. Because delayed fertilization requires long-lived sperm, features of sperm morphology that increase longevity should correlate with presence or absence of delayed fertilization and even the duration of the delay. Increased binding affinity would be important in cases where sperm are stored attached to the uterine lining rather than in specialized vaginal crypts.

Sperm cell performance and structure may bear witness to the presence of post-copulatory sexual selection and can be used to infer sperm competition (Gage, 1998; Anderson & Dixson, 2002; Immler *et al.*, 2007). Morphologies consistent with sperm competition are therefore expected to be found more often in species with delays than in those without. Species in which females mate with more than one male are also expected to exhibit adaptations to sperm competition, so that any comparisons of sperm morphology would need to take mating system dynamics into account. However, because sperm from species with high levels of polyandry might vary in a similar way (also have morphologies consistent with sperm competition) and interfere with this prediction a better study design would also incorporate variation in mating systems. Thus a recommended set-up would include comparisons of sperm from monoandrous and polyandrous species both with and without delayed reproduction (four groups).

Features of sperm that might aid a male's competitive ability include number, size, motility, mid-piece volume, mitochondrial arrangement, amount of ATP (Jeulin & Soufir, 1992; Perchec *et al.*, 1995; Travis *et al.*, 2001) and length (Pitnick *et al.*, 2009). In particular, mid-piece volumes may indicate the quantity of mitochondria that a sperm possesses (with more mitochondria resulting in better motility) (Anderson & Dixson, 2002). Mitochondrial arrangement within the mid-piece may also play a role in sperm longevity and sperm storage capabilities (Wimsatt, Krutzsch & Napolitano, 1966) as mitochondrial respiration capabilities are correlated with successful fertilization (Windsor, 1997).

Increased sperm longevity also extends the time over which sperm would compete for fertilization. Sperm lifespan is known to correlate with the length of female oestrus cycles (Chang & Rowson, 1965; Miyamoto & Chang, 1972) and it is reasonable to expect that co-evolution occurs between

Table 6. Sperm length for species with delayed fertilization compared to those without delayed fertilization (either delayed implantation or no delay)

Order	Species	Common name	Sperm total length (μm)	Delay type	Source		
Chiroptera	<i>Chalinolobus gouldii</i>	Gould's wattled bat	58	Delayed fertilization	See Table 5 for delayed fertilization sources		
	<i>Eptesicus fuscus</i>	Big brown bat	72	Delayed fertilization			
	<i>Lasiurus borealis</i>	Eastern red bat	67.1	Delayed fertilization			
	<i>Myotis lucifugus</i>	Little brown bat	51	Delayed fertilization			
	<i>Myotis sodalis</i>	Indiana bat	65.5	Delayed fertilization			
	<i>Nyctophilus geoffroyi</i>	Lesser long-eared bat	53	Delayed fertilization			
	<i>Perimyotis subflavus</i>	Eastern pipistrelle	86.16	Delayed fertilization			
Carnivora	<i>Canis familiaris</i>	Domestic dog	55.3	Delayed fertilization	See Table 7 for delayed implantation sources		
	<i>Neovison vison</i>	American mink	43	Delayed implantation			
	<i>Ursus arctos</i>	Brown (grizzly) bear	30.7	Delayed implantation			
	<i>Ursus maritimus</i>	Polar bear	36.3	Delayed implantation	Hayssen <i>et al.</i> (1993) and Lindenfors <i>et al.</i> (2003)		
	<i>Ailuropoda melanoleuca</i>	Panda bear	51.2	None*			
	<i>Eupleres goudotii</i>	Falanouc	45	None*			
	<i>Felis catus</i>	Cat	59.35	None*			
	<i>Panthera tigris</i>	Tiger	43.63	None*			
	Perissodactyla	<i>Equus caballus</i>	Horse	60.6		None	Day (1942)
	Primata	<i>Homo sapiens</i>	Human	58.39		None	Bishop (1961)

*indicates that the lack of delayed fertilization was inferred given short periods of oestrus followed by a quick gestation. Data on sperm length are from Cummins & Woodall (1985).

female ability to store sperm and a male's ability to produce long-lived sperm (Parker, 1984). If sperm from several males compete with each other for longevity, such that longer lived sperm have higher chances of fertilization in delaying females, an evolutionary arms race may result, with selection for ever-increasing longevity. Morphology and performance of sperm from monoandrous and polyandrous species with delayed fertilization could be compared to test this prediction. Sperm from species with delayed fertilization do appear to be slightly longer than those from species without delayed fertilization (SPSS one-way ANOVA, $P=0.027$, $N=17$ species, Table 6). However because this analysis does not include potential phylogenetic patterns in sperm length, additional work is needed to make a conclusive statement comparing sperm size in species with and without delays.

Prediction 2: If seminal products aid sperm longevity, we might expect them to be particularly pronounced in delaying species either in quantity or composition. Seminal fluids may have diversified in a manner consistent with a function in sperm competition (Ramm *et al.*, 2008; Lemaître *et al.*, 2011) whereby specific proteins are present in the ejaculate that may aid in sperm-competitive processes. Because components of the ejaculate are important for male-derived copulatory plugs and other aspects of the fertilization process (Aumüller & Seitz, 1990) they present an important avenue for investigations of sexual selection in species with delayed fertilization. The ejaculate itself is an indicator of sexual selection and the composition of seminal fluids in species with delayed fertilization may differ from species without delays in a manner consistent with a role in post-copulatory sexual selection. Research aimed

at understanding how seminal accessory organs (glands) as well as their products differ in taxa with different degrees of sperm competition would be valuable. For example the presence or absence of specific proteins might be informative in the context of sperm competition (see Ramm *et al.*, 2008) and the associated sperm longevity in knockouts compared to individuals producing these seminal proteins. Both Prediction 1 and Prediction 2 could be investigated by performing comparative studies of sperm and associated ejaculate from species both with and without delays. Currently, the seminal fluids of only a limited subset of mammals have been examined and do not include data on species with delays that would allow testing of this hypothesis (Lüpold, 2013).

Prediction 3: The female genital tract may be more elaborate or convoluted (Gomendio & Roldan, 1993), presenting what Eberhard (1996) called 'a torturous route to the egg,' when delays occur in a species. If females from species with delayed fertilization experience more male-driven paternity biases they may be more likely to have crypts, invaginations or other elaborate structures relative to those without delays. These elaborations could act as sperm-storage organs by increasing the surface area of the reproductive tract and potentially providing secure sites for sperm to be maintained and possibly evaluated. It is currently unclear if species with delayed fertilization have elaborated tracts. Some marsupials have vaginal crypts (Bedford, Rodger & Breed, 1984). However, the marsupial taxa with crypts are inconsistent with those that store sperm for longer periods (the latter may have crypts that have remained undescribed). Dogs which have a short period of sperm storage (about

11 days; Birkhead & Møller, 1993) possess uterine glands where sperm are stored (Rijsselaere *et al.*, 2004).

Prediction 4: We expect penile morphology of species with delays to be more elaborate if such morphology functions in sperm competition (sperm removal, placement or displacement). In addition to navigating elaborated female reproductive morphologies (Brennan *et al.*, 2007; Higginson *et al.*, 2012), variation in male genitalia may be required for female stimulation and subsequent cryptic female choice (Eberhard, 1996). Penile elaborations (defined by the presence of fleshy/cartilaginous or ossified extrusions) have been implicated in post-copulatory sexual selection in several species of mammals (Eberhard, 1985; Stockley, 2002; Hosken & Stockley, 2004; Ramm, Parker & Stockley, 2005). The importance of penile spines for stimulating females has been noted in species with induced ovulation (Zarrow & Clark, 1968) but the function in delaying species is expected to be quite different given the disparity between mating and ovulation. The use of male genital features to remove sperm has been demonstrated in damselflies (Waage, 1979), implicated in other insects (Eberhard, 1985), and inferred in mammals (Dixon, 1987; Verrell, 1992; Stockley, 2002; Ferguson & Larivière, 2004; but see Hosken *et al.*, 2001). We suggest that delaying species might use spines to remove sperm from sperm stores. However, in many species we do not know where the penis reaches within the female and thus it is unclear where spines might be utilized. Many species of bats store sperm in the oviducts or at the utero-tubal junction (Uchida & Mori, 1987) but does the penis and its associated spines reach this point? At least in humans glans morphology has been shown to be important in providing a plunger-like effect (Gallup & Burch, 2004) this action could pull sperm to a region where the spines may then serve the suggested function of sperm removal.

Comparing data from artificially inseminated females to data from naturally mating females with known mating orders of males and different degrees of penile (bacular) elaboration would allow an assessment of this prediction. Cryptic female choice due to stimulation *via* male genital elaborations would be extremely difficult to test but is worth further investigation. Finally, comparative analyses of penis size and/or elaboration across taxa with different reproductive physiologies (delay present or absent) may be fruitful for determining if there is any morphological evidence of sexual selection operating on primary sexual characteristics. Species with delays do have spines including *Lasius cinereus* (Table 2) and preliminary examinations suggest several species without delayed fertilization, such as *Carollia perspicillata*, may not have spines (T. J. Orr unpublished data). Relating the placement of spines relative to stored sperm in delaying taxa would be an obvious next step in interpreting these data.

Prediction 5: Species that have delays and simultaneously occurring pregnancies are expected to use delays to fine-tune reproduction and thus have a lower failure of pregnancies (see also Prediction 8). We suggest that species that have co-occurring pregnancies and superfetation (Roellig *et al.*, 2011) should be evaluated. Stockley (2003) found that multiple mating was generally

beneficial for female mammals in that these females exhibited lower rates of reproductive failure. Among the taxa examined several of those with ‘low reproductive failure’ and ‘high multiple mating’ had delayed implantation compared with those that have ‘high reproductive failure’ and ‘low multiple mating’ [for example *Ursus* spp. (delay) compared to *Canis* spp. (no delay)].

Prediction 6: Species with delayed fertilization should exhibit more sperm competition and adaptations relating to sperm competition (e.g. higher sperm counts or greater sperm viability or longevity) than species without delayed fertilization. In species with delayed fertilization, stored sperm, potentially from several males, remain in the female’s reproductive tract for a longer time than in species without delays. Furthermore, this length of time likely increases the opportunity for female remating. Thus, delayed fertilization is expected to enhance the potential for sperm competition.

Increased sperm competition due to higher remating rates in females during delayed fertilization may place selective pressure on males to produce more and/or longer-lived sperm. A positive relationship between testes size and sperm competition risk has been demonstrated in many mammalian taxa, including bats (Hosken, 1997; Wilkinson & McCracken, 2003), primates (Harcourt *et al.*, 1981), zebras (Ginsberg & Rubenstein, 1990), and other mammals (Kenagy & Trombulak, 1986). This is presumably because mammals with larger testes produce more sperm (Willet & Ohms, 1957; Amann, 1970), and sperm are costly to produce (Dewsbury, 1982; Olsson, Madsen & Shine, 1997), so species that do not experience high levels of sperm competition are unlikely to invest in large testes. Thus, species with delayed fertilization are expected to have larger relative testes sizes compared to those without delayed fertilization if they are experiencing more sperm competition. Bats with delayed fertilization have significantly larger testes than those with other types of delays lending some support to this prediction (Orr & Zuk, 2013).

Sperm competition during delayed fertilization could also be measured experimentally. By artificially inseminating females with a mix of sperm from different males, the effects of both sperm number and order would be removed. Observed paternity biases could be evidence of differential male competitive abilities *via* sperm competition. In addition to performing paternity analyses sperm could be labeled with chemical markers to inform us of the degree of mixing between ejaculates of different males within the female’s reproductive tract in species with delayed fertilization (for an example of this type of experiment, see King *et al.*, 2002). These results could be compared to the predictions of sperm competition such as first-male precedence, last-male advantage, and a fair raffle among others (Parker, 1970, 1990).

Prediction 7: Species with delays will exhibit greater paternity biases relative to those species without delays. In species with delayed fertilization not only might males compete *via* sperm competition (Prediction 6) but females would have more time to bias the success of sperm from different males. In some cases biases might be for a certain male or in other instances a suite of males if a heterogenous litter is preferential as

is the case in some species (e.g. heterozygote advantage, bet-hedging in uncertain environments).

Delayed fertilization could facilitate cryptic female choice if, during the period of delay, females initiate processes (e.g. movement of sperm to particularly 'good' storage sites) that enable them to selectively fertilize eggs later. Additionally, in species with variable delay lengths, the duration of delay itself might be expected to correspond to the quality of a male, with near-immediate fertilization when females mate with a high-quality male and a lengthier delay when the mate is less than optimal. This could occur in either obligate or facultative delaying species. Facultative delays may be of variable lengths but variable obligate delays are also seen in some species such as crabeater seals (*Lobodon carcinophagus*; delayed implantation 48–125 days) (Laws, Baird & Bryden, 2003). This strategy could allow a female to hedge her bets and use sperm from lower-quality mates only if no better options become available. Female processes relating to cryptic female choice that may occur during delayed fertilization include multiple egg release, female ejection of sperm or copulatory plug removal. Indeed, differential ovulation, i.e. ovulation only after mating with particular males (Larivière & Ferguson, 2003), may occur during delayed fertilization in some carnivore females.

Empirical evidence consistent with the possibility of cryptic female choice during delays comes from bats (Table 2) in which the female's reproductive tract distinguishes dead eggs from living ones and selectively moves the former out of the oviducts (Rasweiler, 1979; Badwaik & Rasweiler, 2000). This suggests that such complex processes as only allowing particular sperm to fertilize eggs, or removing genetically incompatible blastocysts or those from poor-quality fathers from the reproductive tract, are possible. While these processes are not restricted to species with delayed fertilization, they may be particularly prevalent in such taxa. Similarly, in bat species with delayed fertilization, specialized cells in the female's reproductive tract appear to regulate sperm attachment and release prior to fertilization (Kruttsch, Crichton & Nagle, 1982; Krishna, 1997; Scott, 2000). Unused sperm cells are destroyed by phagocytosis in the spring (Kruttsch *et al.*, 1982; Krishna, 1997).

Female sensitivity to sperm quality offers the potential for differential use of sperm from different males. Many species with delays are polytocous, meaning that more than one egg is released per ovulation, including the roe deer (Vanpé *et al.*, 2009) and members of Chiroptera, Rodentia and Carnivora (Table 2) (Badwaik & Rasweiler, 2000; Stockley, 2003). In species with postpartum oestrus, some reproductive stages can overlap, allowing for the accumulation of eggs from successive ovulations (Stockley, 2003). For example, in *Myotis moluccarum*, only one of several eggs released at ovulation is actually fertilized (Lloyd, Hall & Bradley, 1999). In the Eastern pipistrelle (*Perimyotis subflavus*), a species with delayed fertilization (Guthrie, 1933), only one embryo develops despite the ovulation of multiple eggs (Wimsatt, 1945).

Even in species that only release a single ovum at a time, eggs could overlap within the reproductive tract if

a developing blastocyst is present while ovulation occurs (Scrimshaw, 1944; Roellig *et al.*, 2011). Marsupials are particularly noteworthy in their ability to have various reproductive stages occurring simultaneously (Prediction 5). Reproductive delays in this group are highly correlated with existing pregnancies (Tyndale-Biscoe & Renfree, 1987). This level of reproductive control could allow females to evaluate sperm, zygotes and implanted embryos.

Paternity analyses of species with delayed fertilization would help the evaluation of this prediction. Caution should be taken when trying to disentangle male *versus* female control of paternity as males may also have modes through which paternity is biased; for example *via* sperm competition (Prediction 6) or ejaculates with compounds that might manipulate either other sperm or female physiologies. Currently, studies of paternity are only available for a few mammalian species with delays and are of offspring resulting from a completed pregnancy, which may have biased paternity results. Nevertheless, Soulsbury (2010) lists the frequency of multiple paternities for around 67 species of mammals, including several species with reproductive delays. Definitive lack of reproductive delay is confirmed for only a few of these. Additional population-level paternity studies at an earlier stage (i.e. pre-implantation) are necessary to disentangle the patterns of paternity due to pre- and post-copulatory processes.

Prediction 8: If males are using copulatory plugs as a form of mate guarding, such plugs should be particularly common in species with delayed fertilization and the plugs would be of male rather than female origin. Males of species with delayed fertilization may have a greater use for copulatory plugs, an organic vaginal seal formed after mating from substances produced by either sex (Baumgardner *et al.*, 1982; Tideman, 1993; Keeley & Keeley, 2004). In some mammalian species, these plugs serve as a form of 'mate guarding' and consequently elicit intra-sexual competition (Devine, 1977; Voss, 1979). Copulatory plugs are typically interpreted as a way for males to prevent additional copulations. However, the role of copulatory plugs can be interpreted in the context of their origin: male or female. Plugs produced by females (i.e. from vaginal secretions; Voss, 1979) may be employed to keep sperm sequestered in the reproductive tract; by blocking subsequent ejaculates from reaching the egg, females could control the fate of sperm from lower-quality males. If the vaginal plug is male-derived (i.e. from seminal fluid), it may play a role in male–male competition by preventing other males from mating with the same female. Alternatively, the plug may be used to prevent the female from immediate sperm dumping. Copulatory plugs are expected to be particularly important (and thus more common) in species with delayed fertilization if having a plug decreases likelihood of female re-mating during the delay (passive 'mate guarding') or if it increases likelihood of sperm storage. Female bats have been observed removing copulatory plugs and dumping the sperm from a previous mating [*Rhinolophus ferrumequinum* (Fenton, 1984), *Nyctophilus gouldi* (Phillips & Inwards, 1985) and *Corynorhinus townsendii* (Pearson *et al.*, 1952)]. Penile elaborations such

as spines may also be used to remove copulatory plugs (Armstrong, 2005). Currently the origin (male *versus* female) of plugs has only been examined in a few species and thus it is difficult to say if the data support male or female plug origin in species with delays.

(2) Delays between fertilization and implantation

After fertilization, the zygote begins to develop. Cell division continues until the conceptus becomes a blastocyst. In many species, the blastocyst remains unattached but is maintained in the female's reproductive tract (Table 7). This delay in implantation can last from 21 days (*Miniopterus minor*, the least long-fingered bat; Mori & Uchida, 1980) to over 2 months (*Rhinolophus landeri*, Lander's horseshoe bat; Racey, 1982) or almost a year (*Martes pennanti*, fisher; Wright & Coulter, 1967). Several modes of post-copulatory sexual selection would be facilitated by a greater time frame between fertilization and implantation.

(a) Cryptic female choice via selective implantation, zygote comparison, and re-absorption

By delaying implantation, females may allow for the accumulation and comparison of zygotes. The female might also fail to prepare the uterus for an embryo by foregoing a luteal cycle (Eberhard, 1996) and as a consequence reject embryos from particular males. During this stage the selective re-absorption of some embryos may also occur. In some mammals, including some Carnivora, females re-absorb embryos (Larivière & Ferguson, 2003), and re-absorption may be aimed at specific embryos or blastocysts. In the bat *Pipistrellus rusticus*, about four blastocysts co-occur in the tract, but only one or two implant (van der Merwe & Rautenbach, 1990), while in *Perimyotis subflavus*, up to seven eggs are fertilized but only one implants (Wimsatt, 1945; Table 2). A useful strategy in species that have small litters, including those bats that typically only have one or two offspring per litter (Barclay & Harder, 2003), could be to allow multiple fertilization events, facilitating the comparison of blastocysts. A similar concept of overproduction of young as a strategy to maintain female reproductive success has been discussed in reference to the production of eggs and asynchronous hatching in birds (Konarzewski, 1993).

Between fertilization and implantation, zygotes possessing incompatible combinations of genes could fail to implant and this process might be refined during delayed implantation. Thus, during delays post-copulatory sexual selection may also operate *via* genetic incompatibility avoidance (Tregenza & Wedell, 2000). Zeh & Zeh (1996, 1997, 2000) suggested that females may passively reject embryos that have undesirable genetic patterns. This process is dictated by genetic compatibility of the female and male genomes when combined in the new zygote, and may be due to several processes, including immune system interactions, intra and intergenomic conflict, dominance, over-dominance and embryo–maternal interactions (Zeh & Zeh, 1996, 1997; Tregenza & Wedell, 2000; Stockley, 2003). In turn,

delays might serve as 'check points' for a pregnancy to continue to the next stage of development, or as a point of assessment during which genetic incompatibility is assessed. For example, if a zygote's genetic makeup can only be detected in mature blastocysts, we could expect females of species with delayed implantation to be evaluating the genetic compatibility of their blastocysts during the delay.

Indirect support of this idea comes from a comparative study of polytocous mammals (those with litters rather than a single offspring), which revealed that species in which females mate multiply (and have numerous eggs available for fertilization) have lower rates of reproductive failure than do monogamous species (Stockley, 2003). This result supports the role of genetic incompatibility avoidance, presumably through the comparison of fertilized eggs (Stockley, 2003). A longer period prior to implantation would allow time for female assessment of the developing conceptus and the realized combination of maternal and paternal genomes. As the conceptus develops any genetic incompatibilities may become more obvious.

(b) Predictions and experiments: delayed implantation

Prediction 9: Females of species with delayed implantation will exhibit a higher frequency of post-copulatory choice among blastocysts than females of species without such delays. We also expect delays to offer females a longer window in which to evaluate offspring and thus that females with delayed implantation will have lower reproductive failure than those without delays. Evidence for multiple paternity within litters of twinning bats and other mammals is accumulating (Table 2), consistent with several blastocysts of different origins co-occurring in the female's reproductive tract, even in species that usually only give birth to twins or a single offspring (Vonhof *et al.*, 2006; Fox, Spencer & O'Brien, 2008). If females exhibit delays of variable lengths they may allow some blastocysts to implant immediately after mating with a high-quality male while blastocysts from low-quality males may remain in the reproductive tract. Embryos of different sizes that may be a result of different implantation times have been noted in numerous taxa and are often mistaken for superfetation (Roellig *et al.*, 2011). Caution must be taken to not confound natural *versus* sexual selection in interpreting results associated with this prediction.

(3) Delays between implantation and birth (delayed development)

In a few species of bats (and possibly other taxa), development may be slowed or stop completely after implantation (Table 8).

(a) Predictions and experiments: delayed development

Prediction 10: If delayed development facilitates post-copulatory sexual selection, species with delayed development should exhibit lower degrees of late-stage reproductive failure. If females are able to accumulate and compare developing embryos during reproductive delays, they may have more opportunities to

Table 7. Species known to exhibit delayed implantation with length of delay (if known). According to Tyndale-Biscoe & Renfree (1987) all macropods except *Macropus fuliginosus* have delayed implantation

Order	Family	Species	Common name	Delay length (days)	Source
Artiodactyla (Cetartiodactyla)					
	Cervidae	<i>Capreolus capreolus</i>	European roe deer	135	Ziegler (1843) and Bischoff (1854)
		<i>Elaphurus davidianus</i>	Père David's deer	*implicated	Brinklow & Loudon (1993)
Carnivora					
	Ailuridae	<i>Ailurus fulgens</i>	Red panda	*implicated	Roberts & Gittleman (1984)
	Mephitidae	<i>Conepatus mesoleucus</i>	Western hog-nosed skunk	60	MacDonald (1984)
		<i>Mephitis macroura</i>	Hooded skunk	30	MacDonald (1984)
		<i>Mephitis mephitis</i>	Striped skunk	30	Wade-Smith & Richmond (1975, 1978) and Wade-Smith <i>et al.</i> (1980)
		<i>Spilogale gracilis</i>	Western spotted skunk	150	Mead (1968a,b, 1981) and Greensides & Mead (1973)
	Mustelidae	<i>Arctonyx collaris</i>	Hog badger	—	Parker (1979)
		<i>Enhydra lutris</i>	Sea otter	130	Novikov (1956) and Sinha, Conaway & Kenyon (1966)
		<i>Gulo gulo</i>	Wolverine	210	*may be facultative Wright & Rausch (1955) and Rausch & Pearson (1972)
		<i>Lontra longicaudis</i>	Neotropical river otter	*may be facultative	Cubas <i>et al.</i> (1993) and Jacome & Parera (1995)
		<i>Lutra canadensis</i>	American river otter	285	Hamilton & Eadie (1964)
		<i>Martes americana</i>	American marten	225	Ashbrook & Hanson (1930), Pearson & Enders (1944) and Wright (1963)
		<i>Martes flavigula</i>	Yellow-throated marten	105	Roberts (1977)
		<i>Martes foina</i>	Beech marten	240	Prell (1927) and Canivenc <i>et al.</i> (1981)
		<i>Martes gwatkinsii</i>	Nilgiri marten	—	MacDonald (1984)
		<i>Martes martes</i>	Pine marten	240	Prell (1927), Stubbe (1968) and Canivenc <i>et al.</i> (1981)
		<i>Martes melampus</i>	Japanese marten	195	MacDonald (1984)
		<i>Martes pennanti</i>	Fisher	315	Enders & Pearson (1943) and Eadie & Hamilton (1958)
		<i>Martes zibellina</i>	Sable	247	Novikov (1956) and Bernatskii, Snytko & Nosova (1976)
		<i>Meles meles</i>	Eurasian badger	255	Fries (1880), Neal & Harrison (1958), Canivenc (1966) and Canivenc & Bonnin (1981)
		<i>Mellivora capensis</i>	Honey badger	*implicated	Rosevear (1974)
		<i>Mustela erminea</i>	Short-tailed weasel, ermine	270	Wright (1942)
		<i>Mustela frenata</i>	Long-tailed weasel	240	Wright (1942)
		<i>Mustela lutreola</i>	European mink	8.5	Nowak & Paradiso (1983)
		<i>Mustela (Neovision) vison</i>	American mink	27.5	Hansson (1947) and Enders (1952)
		<i>Taxidea taxus</i>	American badger	195	Hamlett (1932b) and Wright (1966)
		<i>Vormela peregusna</i>	Marbled polecat	223	Mendelssohn, Ben-David & Hellwing (1988)
	Odobenidae	<i>Odobenus rosmarus</i>	Walrus	135	Fay (1981, 1982)
	Otariidae	<i>Arctocephalus australis</i>	South American fur seal	120	Riedman (1990)
		<i>Arctocephalus philippii</i>	Juan Fernández fur seal	*implicated	Riedman (1990)
		<i>Arctocephalus galapagoensis</i>	Galápagos fur seal	*implicated	Riedman (1990)
		<i>Arctocephalus gazella</i>	Antarctic fur seal	126	Riedman (1990)
		<i>Arctocephalus pusillus</i>	Cape fur seal, South African fur seal	~120	Riedman (1990)
		<i>Arctocephalus townsendi</i>	Guadalupe fur Seal	120	Riedman (1990)
		<i>Arctocephalus tropicalis</i>	Subantarctic fur seal	129	Riedman (1990)
		<i>Callorhinus ursinus</i>	Northern fur seal	120	Craig (1964) and Daniel (1981)
		<i>Eumetopias jubatus</i>	Steller's sea lion	105	Harrison (1969) and Schusterman (1981)
		<i>Neophoca cinerea</i>	Australian sea lion	*implicated	Riedman (1990)

Table 7. Continued

Order	Family	Species	Common name	Delay length (days)	Source
		<i>Otaria byronia</i>	Southern sea lion, or South American sea lion	105	Hamilton (1939) and Daniel (1981)
		<i>Phocartos hookeri</i>	Hooker's sea lion	—	Riedman (1990)
		<i>Zalophus californianus</i>	California sea lion	97.5	Odell (1981)
		<i>Cystophora cristata</i>	Hooded seal	105	Ørtisland (1964)
		<i>Erignathus barbatus</i>	Bearded seal	75	McLaren (1958) and Harrison (1969)
		<i>Halichoerus grypus</i>	Grey seal	105	Hewer & Backhouse (1968) and Harrison (1969)
		<i>Hydrurga leptonyx</i>	Leopard seal	48	Sinha & Erickson (1972) and Riedman (1990)
		<i>Leptonychotes weddellii</i>	Weddell seal	75	Mansfield (1958), Stirling (1969) and Kooyman (1981)
		<i>Lobodon carcinophagus</i>	Crabeater seal	60	Harrison (1969) and Daniel (1981)
		<i>Mirounga angustirostris</i>	Northern elephant seal	75	Steward & Huber (1993)
		<i>Mirounga leonina</i>	Southern elephant seal	105	Harrison, Matthews & Roberts (1952) and Laws (1956)
	Phocidae	<i>Monachus monachus</i>	Mediterranean monk seal	*implicated	Riedman (1990)
		<i>Monachus schauinslandi</i>	Hawaiian monk seal	*implicated	Riedman (1990)
		<i>Ommatophoca rossii</i>	Ross seal	~75	Reeves & Ling (1981) and Kovacs & Lavigne (1986)
		<i>Pagophilus groenlandicus</i>	Harp seal	105	Harrison (1963, 1969)
		<i>Pusa (Phoca) caspica</i>	Caspian seal	*implicated	Riedman (1990)
		<i>Pusa (Histriophoca) fasciata</i>	Ribbon seal	*implicated	Riedman (1990)
		<i>Pusa (Phoca) hispida</i>	Ringed seal	105	McLaren (1958), Harrison (1969) and Frost & Lowry (1981)
		<i>Pusa (Phoca) largha</i>	Larghe, spotted seal	75	Bigg (1981) and Harrison (1969)
		<i>Pusa (Phoca) sibirica</i>	Baikal seal	—	Kozhov (1947) and Riedman (1990)
		<i>Pusa (Phoca) vitulina</i>	Harbor seal	~60	Fisher (1954), Harrison (1963, 1969) and Bigg & Fisher (1974)
	Ursidae	<i>Helarctos malayanus</i>	Sun bear	*implicated	Dathe (1963) and McCusker (1974)
		<i>Melursus ursinus</i>	Sloth bear	—	Laurie & Seidensticker (1977) and Puschman, Schuppel & Kronberger (1977)
		<i>Ursus americanus</i>	American black bear	165	Hamlett (1935) and Wimsatt (1963)
		<i>Ursus arctos</i>	Brown (grizzly) bear	150	Dittrich & Kronberger (1963)
		<i>Ursus maritimus</i>	Polar bear	240	Dittrich (1961) and Volf (1963)
	Viverridae	<i>Civettictis civetta</i>	African civet	~20 *implicated	Ewer & Wemmer (1974)
Chiroptera	Pteropodidae	<i>Cynopterus brachyotis</i>	Lesser short-nosed fruit bat	—	Kofron (1997)
		<i>Cynopterus minutus</i>	Minute fruit bat	—	Kofron (1997)
	Rhinolophidae	<i>Rhinolophus landeri</i>	Lander's horseshoe bat	60	Racey (1982)
		<i>Rhinolophus rouxi</i>	Rufous horseshoe bat	43	Ramakrishna & Rao (1977) and Racey (1982)
	Vespertilionidae	<i>Corynorhinus townsendii</i>	Townsend's big-eared bat	*implicated	Pearson <i>et al.</i> (1952)
		<i>Lasionycteris noctivagans</i>	Silver-haired bat	10	Druecker (1972)
		<i>Miniopterus australis</i>	Little long-fingered bat	30	Racey (1982)
		<i>Miniopterus fraterculus</i>	Lesser long-fingered bat	~135	Racey (1982)
		<i>Miniopterus minor</i>	Least long-fingered bat	21	Mori & Uchida (1980)
Cingulata	Dasyopodidae	<i>Dasyopus hybridus</i>	Mulita armadillo	60	Hamlett (1932 <i>a</i> , 1935) and Enders (1966)
		<i>Dasyopus novemcinctus</i>	Nine-banded armadillo	120	Hamlett (1932 <i>b</i> , 1935) and Enders (1966)
Diprotodontia	Acrobatidae	<i>Acrobates pygmaeus</i>	Feathertail glider	—	Ward & Renfree (1988)

Table 7. Continued

Order	Family	Species	Common name	Delay length (days)	Source
		<i>Distoechurus pennatus</i>	Feathertailed possum	—	Ward & Renfree (1988) and Ward (1990)
	Burramyidae	<i>Cercartetus concinnus</i>	Western pygmy-possum	—	Ward (1990)
		<i>Cercartetus lepidus</i>	Little pygmy-possum	—	Ward (1990)
		<i>Cercartetus nanus</i>	Eastern pygmy-possum	—	Ward (1990)
	Macropodidae	<i>Lagostrophus fasciatus</i>	Banded hare-wallaby	—	G. B. Sharman (unpublished data) cited in Sharman (1963)
		<i>Macropus agilis</i>	Agile wallaby	—	Merchant (1976)
		<i>Macropus eugenii</i>	Tammar wallaby	< 330	Renfree (1994)
		<i>Macropus giganteus</i>	Eastern grey kangaroo	—	Kirkpatrick (1965), Poole & Catling (1974) and Poole (1975)
		<i>Macropus parma</i>	Parma wallaby	~31	Maynes (1973)
		<i>Macropus parryi</i>	Pretty-faced (whiptail) wallaby	—	Maynes (1973)
		<i>Macropus robustus</i>	Common wallaroo, eastern wallaroo	35	Ealey (1963)
		<i>Macropus rufogriseus</i>	Red-necked wallaby	*may be facultative	Buchanan (1963)
		<i>Macropus rufus</i>	Red kangaroo	*may be facultative	Merchant & Calaby (1981)
		<i>Protemnodon eugenii</i>	Kangaroo island wallaby	—	Sharman (1955a)
		<i>Protemnodon ruficollis</i>	Bennett's wallaby	—	Sharman (1955a)
		<i>Setonix brachyurus</i>	Quokka	*may be facultative	Sharman (1955b) and Shield (1968)
		<i>Thylogale billardierii</i>	Tasmanian pademelon, red-bellied pademelon	—	G. B. Sharman (unpublished data) cited in Sharman (1963) and Rose & McCartney (1982)
		<i>Thylogale thetis</i>	Red-necked pademelon	—	G. B. Sharman (unpublished data) cited in Sharman (1963)
		<i>Wallabia bicolor</i>	Swamp wallaby	—	Calaby and Poole (1971)
	Potoroidae	<i>Aepyprymnus rufescens</i>	Rufous bettong	—	Flynn (1930)
		<i>Bettongia cuniculus</i>	Pygmy possum	—	Rose (1978)
		<i>Bettongia gaimardi</i>	Tasmanian bettong	—	Rose (1978)
		<i>Bettongia lesueur</i>	Boodie, burrowing bettong, coccyx	—	Tyndale-Biscoe (1968)
		<i>Bettongia penicillata</i>	Woylie, brush-tailed bettong	—	Parker (1977)
		<i>Potorous tridactylus</i>	Long-nosed potoroo	—	Hughes (1962a) and Shaw & Rose (1979)
	Tarsipedidae	<i>Tarsipes rostratus</i>	Honey possum	*slow	Shaw & Rose (1979) and Renfree (1980)
Eulipotophyla					
	Soricidae	<i>Sorex araneus</i>	Common shrew	—	Brambell (1935)
	Talpidae	<i>Talpa altaica</i>	Altai mole	—	Baevskii (1967) and Judin (1974)

*indicates that the presence of delayed implantation was inferred given long gestation lengths and in several cases closely related species also exhibiting delayed implantation. *facultative' indicates taxa whereby the delay may be dependant upon external factors but insufficient data are available to determine if the delay is obligate or facultative.

carry a high-quality pup successfully to full term. Stockley (2003) suggested that multiply mating females are less likely to experience reproductive failure because they will have higher potential for genetically diverse and thus compatible offspring. Tests of this prediction include comparing per cent of successfully weaned pups from delaying *versus* non-delaying species.

VI. ADDITIONAL CONSEQUENCES OF DELAYS

(1) Life history consequences of delays

The evolution of delays should be considered in relation to their potential costs. For example, delaying fertilization

might result in loss of sperm viability during storage through the degradation of sperm and associated genetic materials. Ants incur immune costs during sperm storage (Baer, Armitage & Boomsma, 2006) and it is plausible that female mammals experience similar costs. Species delaying implantation rather than fertilization may incur some costs associated with maintaining the endometrium or depressing immunity to maintain the blastocysts. Thus, while in general little energetic investment has been made in the unimplanted blastocysts these other costs may make this a more demanding process than delaying fertilization. The immune system is suppressed during pregnancy (Weetman, 1999; Luppi, 2003) and immunological costs may therefore occur during delayed fertilization and delayed development by virtue of extending

Table 8. Species known to exhibit delayed development listed with length of delay

Order	Family	Species	Common name	Delay length (days)	Source
Chiroptera					
Emballonuridae		<i>Saccopteryx bilineata</i>	Greater sac-winged bat	—	Bradbury & Vehrencamp (1976, 1977)
Molossidae		<i>Otopteropus cartilagonodus</i>	Luzon fruit bat	*implicated	Heideman <i>et al.</i> (1993)
Natalidae		<i>Natalus stramineus</i>	Mexican funnel-eared bat	*implicated	Mitchell (1965)
Phyllostomidae		<i>Artibeus jamaicensis</i>	Jamaican fruit bat	75	Fleming (1971)
		<i>Carollia perspicillata</i>	Seba's short-tailed fruit bat	50	Rasweiler & Badwaik (1997)
		<i>Macrotus californicus</i>	California leaf-nosed bat	135	Bleier (1975)
Pteropodidae		<i>Haplonycteris fischeri</i>	Philippine pygmy fruit bat	135	Heideman (1989)
Rhinolophidae		<i>Rhinolophus hipposideros</i>	Lesser horseshoe bat	—	Kolb (1950)
Vespertilionidae		<i>Myotis myotis</i>	Mouse-eared bat	—	Petri <i>et al.</i> (1997)
		<i>Pipistrellus pipistrellus</i>	Common pipistrelle	—	Pagenstecher (1859) and Racey & Potts (1970)

this period of suppression. During delayed development, females may also experience some costs associated with the metabolic demands of the developing embryo. These costs are expected to be lower if delays occur early in gestation relative to later during the embryo's development. The costs of maintaining embryos may explain in part why delayed development is less common than other types of delays.

(2) Post-copulatory sexual selection and the evolution of delays

The potential fitness advantages to females experiencing female-driven post-copulatory sexual selection during reproductive delays may have exciting evolutionary implications. If by lengthening the stages of reproduction, females were better equipped to manipulate paternity in a manner that would benefit them, longer durations of delays may be selected. It is even possible that sexual selection was in part responsible for the evolutionary origins of reproductive delays.

Specifically, selection may have favoured delays because of the benefits to females. These include bet-hedging, defence against genetically incompatible sperm or offspring, and sexual conflict resolution or intensity which may not be directly beneficial for either sex. Bet-hedging, or minimizing risk may be important in taxa with uncertain mating opportunities, whereby females would benefit from being receptive to high-quality mates when they are available (Sandell, 1990). By mating even with poor-quality males, the female would have sperm available in the event that no other mates became available. Alternatively, if a higher quality male came along, she could use post-copulatory sexual selection to select between sperm/progeny. Another form of bet-hedging might include producing a range of offspring phenotypes (by acquiring matings from multiple males) which may allow females to maintain fecundity without risking reproductive failure due to poor sperm or genetic incompatibility.

Similarly, infertility of some sperm might be an issue for females that do not store sperm for extended periods and have short fertile periods. Again, delays might be selected under this situation, allowing females to secure various sperm during the extended period over which she is receptive,

ensuring that some will be fertile. Of course, this assumes that males are able to produce long-lived sperm which may not always be true; fertility usually decreases with sperm age, which would complicate this prediction.

Because male quality is not always apparent at the phenotypic level, females may use delays as an extended period within which to prevent themselves from carrying embryos from certain fathers to full term. Indeed, females that have delays may have more time to assess offspring quality and if delaying females gave birth to higher quality young, they would be at a selective advantage. This idea was presented by Heideman (1988), who suggested that females might gain fitness advantages by being able to re-absorb some embryos selectively. It is possible that delays may also allow the reabsorption of embryos that are genetically incompatible (Zeh & Zeh, 2000). Genetic incompatibility would include cases whereby females benefit from multiple fertilization events so the resulting conceptuses can be evaluated in the context of the resulting genome (maternal and paternal combination) and only those conceptuses with successful combinations allowed to continue developing.

In species where females use delays as a means of biasing paternity, we might expect males to counteract female measures by processes described above. In response, females may evolve additional tactics or lengthen delays to secure increased opportunities for control of post-copulatory events. Furthermore, if females change the timing of events like sperm storage, males must 'follow' or be left in the proverbial dust and thus they are expected to counter-adapt. Females may thus become increasingly dependent on the period of delay for sorting out genetically incompatible sperm, blastocysts or embryos.

(a) Predictions and experiments: post-copulatory sexual selection and the potential evolution of delays

Prediction 11: The length of delays in species with extreme sexual conflict will be greater than in those with lower degrees of conflict. Sexual conflict is expected to play a role in shaping reproductive delays. For example, male adaptations for sperm competition, such as penile elaborations or increased

testes size may be countered by selection on females for longer delays during which cryptic female choice (a female process) might occur. Males may in turn counter with additional novel or exaggerated traits. Thus species with delays may have increased sexual conflict and one possible implication/evolutionary by-product could be an increased length of delays. A decrease in length of delay seems less likely given that delays occur within the confines of the reproductive tract and the extended length of delay may facilitate cryptic female choice however this possibility cannot be excluded.

Prediction 12: If delays have important evolutionary significance via post-copulatory sexual selection, we might expect them to serve as a post-zygotic isolation mechanism relevant for speciation. In species with different reproductive physiologies (delays) cycles between diverging species may become mis-matched which might be an important mechanism for speciation reinforcement. For example, if two recently diverged incipient species were to come back into contact and delays were already used by females as a means of post-copulatory sexual selection (scrutiny of male sperm or offspring genotypes), females of species with delays may have greater opportunities to prevent 'foreign sperm' from fertilizing their precious eggs or have more elaborate mechanisms in place to prevent investment in hybrid offspring (genetic incompatibility avoidance). This prediction would be best examined in recently diverged species or in species with facultative delays that vary by a fixed extrinsic factor like latitude. Gametic isolation could also be examined using artificial insemination of females with sperm from males of diverging taxa following the methods of Ludlow & Magurran (2006). Paternity analysis both of resulting offspring and aborted embryos aimed at determining if paternity biases occur would allow researchers to determine if gametic isolation is occurring.

Alternatively, if delays evolve after a split in incipient species, this change in reproductive physiology itself could result in a barrier to cross-population reproduction. While the possible role of delays for speciation reinforcement has not been examined it is interesting to note that in some cases closely related species often differ in the presence or absence of delays particularly amongst the Carnivora (Lindénfors *et al.*, 2003). For example, western spotted skunks delay implantation while their congeners, eastern spotted skunks, do not (Mead, 1968*a,b*).

VII. CONCLUSIONS

(1) Reproductive delays are temporal pauses in reproduction that occur between mating and fertilization, between fertilization and implantation of the embryo, or after an embryo has implanted. This unique but not uncommon type of mammalian reproduction may offer an unconsidered avenue for the operation of post-copulatory sexual selection because delays lengthen the reproductive periods over which post-copulatory sexual selection operates.

(2) Delayed fertilization (female sperm storage or delayed ovulation) may increase the opportunity for sperm

competition and sperm selection, and in species with delayed implantation, cryptic female choice can operate more freely. Delayed implantation may allow females to bet-hedge by mating with multiple males before committing to a pregnancy. Species that have delayed development are presented with an extended period over which the embryo may be evaluated.

(3) Delays may prove an important factor in explaining phenomena such as bacular size variation (Hosken *et al.*, 2001; Lüpold, McElligott & Hosken, 2004) or the evolution of penile elaborations. Furthermore, including delays as a covariate may help elucidate previously confusing results in studies of mammalian post-copulatory sexual selection. Because females with delays have a longer time frame in which processes such as sperm selection or embryo re-absorption can occur, reproductive delays may provide a new and interesting way to look for cryptic female choice. While we review the implications of delayed reproduction in mammals, similar reproductive physiologies are observed in non-mammalian taxa and significant parallels in the predictions for increased post-copulatory sexual selection presented here are likely.

VIII. ACKNOWLEDGEMENTS

We would like to thank P. Brennan, E. Charnov, E. Dlugosz, A. Furness, T. Garland Jr., K. A. Hammond, V. Haysen, P. Heideman, D. J. Hosken, C. Oufiero, P. Racey, D. Reznick, M. Soley and J. J. Rasweiler IV for insightful exchanges. We also thank two anonymous reviewers for comments that improved the quality of this manuscript. T. J. O. was supported by an American Society of Mammalogy Grant in Aid of Research, the UCR Loomer and Newell Awards, a UC President's Dissertation-Year Fellowship and UC Mexus grant. During the publication process T. J. O. was supported in part by the National Science Foundation Postdoctoral Research Fellowship in Biology under Grant No. (DBI-297 1202871). M. Z. is supported by grants from the National Science Foundation.

IX. REFERENCES

- ALLEN, G. M. (1939). *Bats*. Harvard University Press, Cambridge.
- AMANN, R. P. (1970). Sperm production rates. In *The Testis* (eds A. P. JOHNSON and W. R. GOMES), pp. 433–482. Academic Press, New York.
- ANDERSON, J. A. & DIXSON, A. F. (2002). Sperm competition: motility and the midpiece in primates. *Nature* **416**, 496.
- ARMSTRONG, K. N. (2005). A description and discussion of the penile morphology of *Rhinonictus aurantius* (Gray, 1845) (Microchiroptera: Hipposideridae). *Australian Mammalogy* **27**, 161–167.
- ARNQVIST, G. & ROWE, L. (2005). *Sexual Conflict*. Princeton University Press, Princeton.
- ASHBROOK, F. G. & HANSON, K. B. (1930). *The Normal Breeding Season and Gestation Period of Martens* (Volume 107C). U.S. Department of Agriculture Circular, Washington.
- AUMÜLLER, G. & SEITZ, J. (1990). Protein secretion and secretory processes in male accessory sex glands. *International Review of Cytology* **121**, 127–231.
- BADWAIK, N. K. & RASWEILER, J. J. IV (2000). Pregnancy. In *Reproductive Biology of Bats* (eds E. G. CRICHTON and P. H. KRUTZSCH), pp. 221–293. Academic Press, London.
- BAER, B., ARMITAGE, S. A. O. & BOOMSMA, J. (2006). Sperm storage induces an immunity cost in ants. *Nature* **441**, 872–875.

- BAEVSKII, Y. U. B. (1967). Cytometric and karyometric investigations on the blastocyst of the mole (*Talpa altaica*). *Doklady Akademii Nauk SSSR* **176**, 1198–1200.
- BAKER, J. R. & BIRD, T. F. (1936). The seasons in a tropical rain-forest (New Hebrides): Part 4. Insectivorous bats. *Zoological Journal of the Linnean Society* **40**, 143–161.
- BALLINGER, R. E. (1979). Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. *Ecology* **60**, 901–909.
- BARCLAY, R. M. R. & HARDER, L. D. (2003). Life histories of bats: life in the slow lane. In *Bat Ecology* (eds T. H. KUNZ and M. B. FENTON), pp. 209–256. University of Chicago Press, Chicago.
- BARTHOLOMEW, G. A. (1970). A model for the evolution of pinniped polygyny. *Evolution* **24**, 546–559.
- BAUMGARDNER, D. J., HARTUNG, T. G., SAWREY, D. K., WEBSTER, D. G. & DEWSBURY, D. A. (1982). Muroid copulatory plugs and female reproductive tracts: a comparative investigation. *Journal of Mammalogy* **63**, 110–117.
- BEDFORD, J. M., RODGER, J. C. & BREED, W. G. (1984). Why so many mammalian spermatozoa – a clue from marsupials? *Proceedings of the Royal Society of London* **1223**, 221–233.
- BERGER, P. J. (1966). Eleven month “embryonic diapause” in a marsupial. *Nature* **211**, 435–436.
- BERNARD, R. T. F. & CUMMING, G. S. (1997). African bats: evolution of reproductive patterns and delays. *Quarterly Review of Biology* **72**, 253–274.
- BERNATSKII, V. G., SNYTKO, E. G. & NOSOVA, H. G. (1976). Natural and induced ovulation in the sable (*Martes zibellina* L.). *Doklady Akademii Nauk SSSR* **230**, 1238–1239.
- BEWLEY, J. D. (1997). Seed germination and dormancy. *Plant Cell* **9**, 1055–1066.
- BIGG, M. A. (1981). Harbor seal—*Phoca vitulina* and *P. largha*. In *Handbook of Marine Mammals* (Volume II, eds S. H. RIDGWAY and R. J. HARRISON), pp. 1–27. Academic Press, London.
- BIGG, M. A. & FISHER, H. D. (1974). The reproductive cycle of the female harbor seal of southeastern Vancouver Island. In *Functional Anatomy of Marine Mammals* (Volume II, ed. R. J. HARRISON), pp. 329–347. Academic Press, London.
- BININDA-EMONDOS, O. R. P., CARDILLO, M., JONES, K. E., MACPHEE, R. D. E., BECK, R. M. D., GREYER, R., PRICE, S. A., VOS, R. A., GITTLEMAN, J. L. & PURVIS, A. (2007). The delayed rise of present-day mammals. *Nature* **446**, 507–513.
- BIRKHEAD, T. R. (2000). *Promiscuity*. Harvard University Press, Cambridge.
- BIRKHEAD, T. R. & APPLETON, A. C. (1998). Appendix I. Multiple paternity in mammals. In *Sperm Competition and Sexual Selection* (eds T. R. BIRKHEAD and A. P. MØLLER), pp. 752–755. Academic Press, San Diego.
- BIRKHEAD, T. R. & MØLLER, A. P. (1993). Sexual selection and the temporal separation of reproductive events: sperm storage data from reptiles, birds and mammals. *Biological Journal of the Linnean Society* **50**, 295–311.
- BISCHOFF, T. L. W. (1854). *Entwicklungsgeschichte des Rehes*. J. Richersche Buchhandlung, Giessen.
- BISHOP, D. W. (1961). Biology of spermatozoa. In *Sex and Internal Secretions* (Volume II, ed. W. C. YOUNG), pp. 70–795. Balliere, Tindall & Cox, London.
- BLEIER, W. J. (1975). *Fine structure of implantation and the corpus luteum in the California Leaf-nosed bat, Macrotus californicus*. PhD Thesis: Texas Tech University.
- BOUCHARD, S., ZIGOURIS, J. & FENTON, M. B. (2001). Autumn mating and likely reabsorption of an embryo by a hoary bat, *Lasiurus cinereus* (Chiroptera: Vespertilionidae). *American Midland Naturalist* **145**, 210–212.
- BRADBURY, J. W. & VEHCAMP, S. L. (1976). Social organization and foraging in Emballonurid bats. *Behavioral Ecology and Sociobiology* **1**, 337–381.
- BRADBURY, J. W. & VEHCAMP, S. L. (1977). Social organization and foraging in Emballonurid bats III. Mating systems. *Behavioral Ecology and Sociobiology* **2**, 1–18.
- BRAMBELL, F. W. R. (1935). Reproduction in the common shrew (*Sorex araneus* Linnaeus) I. The oestrus cycle of the female. *Philosophical Transactions of the Royal Society of London, Series B* **225**, 1–49.
- BRENNAN, P. L. R., PRUM, R. O., MCCracken, K. G., SORENSON, M. D., WILSON, R. E. & BIRKHEAD, T. R. (2007). Coevolution of male and female genital morphology in waterfowl. *PLoS ONE* **5**, 1–6.
- BRINKLOW, B. R. & LOUDON, A. S. (1993). Gestation periods in the Pere David's Deer (*Elaphurus davidianus*): evidence for embryonic diapause or delayed development. *Reproduction, Fertility and Development* **5**, 567–575.
- BUCHANAN, G. D. (1963). Probable delayed implantation in Bennett's wallaby. *Journal of Mammalogy* **44**, 430–431.
- CALABY, J. H. & POOLE, W. E. (1971). Keeping kangaroos in captivity. *International Zoo Yearbook* **11**, 5–12.
- CANIVENC, R. (1966). A study of progestation in the European badger (*Meles meles* L.). *Symposia of the Zoological Society of London* **15**, 15–26.
- CANIVENC, R. & BONNIN, M. (1981). Environmental control of delayed implantation in the European badger (*Meles meles*). *Journal of Reproduction and Fertility, Supplement* **29**, 25–33.
- CANIVENC, R., MAUGET, C., BONNIN, M. & AITKEN, R. J. (1981). Delayed implantation in the beech marten (*Martes foina*). *Journal of Zoology, London* **193**, 325–332.
- CHANG, M. C. & ROWSON, L. E. A. (1965). Fertilization and early development of Dorset Horn sheep in the spring and summer. *Anatomical Record* **152**, 303–316.
- CHRISTIAN, J. J. (1956). The natural history of a summer aggregation of the big brown bat. *Eptesicus fuscus fuscus*. *American Midland Naturalist* **55**, 66–95.
- CLARK, M. J. (1966). The blastocyst of the red kangaroo, *Megaleia rufa* (Desm.), during diapause. *Australian Journal of Zoology* **14**, 19–25.
- CONOWAY, C. H. (1955). Embryo reabsorption and placental scar formation in the rat. *Journal of Mammalogy* **3**, 516–532.
- CRAIG, A. M. (1964). Histology of reproduction and the oestrus cycle in the female fur seal, *Callorhinus ursinus*. *Journal of Fisheries Research Board of Canada* **21**, 773–811.
- CUBAS, Z. S., FRANCISCO, L. R., GOMES, M. L. F., HOERNER, P. G., LEITE, M. H. P., RUTZ, A. Jr., SILVA, A. S. F., SILVA, M. E. P. F. & SUTTI, L. M. (1993). Criação de lontra (*Lutra longicaudis*) no Zoológico de Curitiba. *Informativo ABRAVAS* **3**, 1.
- CUMMINS, J. M. & WOODALL, P. F. (1985). On mammalian sperm dimensions. *Journal of Reproduction and Fertility* **75**, 153–175.
- DAY, F. T. (1942). Survival of spermatozoa in the genital tract of the mare. *Journal of Agricultural Science* **32**, 108–111.
- DANIEL, J. C. J. (1970). Dormant embryos of mammals. *Bioscience* **20**, 411–415.
- DANIEL, J. C. J. (1981). Delayed implantation in the northern fur seal (*Callorhinus ursinus*) and other pinnipeds. *Journal of Reproduction and Fertility, Supplement* **29**, 35–50.
- DARWIN, C. (1859). *On the Origin of Species by Means of Natural Selection*. Murray, London.
- DATHE, H. (1963). Beitrag zur Fortpflanzungsbiologie des Malaia Baeren, *Helarctos M. malayanus* (Raffl.). *Zeitschrift für Säugetierkunde* **28**, 155–162.
- DEVINE, M. C. (1977). Copulatory plugs, restricted mating opportunities and reproductive competition among male garter snakes. *Nature* **267**, 345–346.
- DEWSBURY, D. A. (1982). Ejaculate cost and male choice. *American Naturalist* **119**, 601–610.
- DITTRICH, L. (1961). Zur Wurfzeit des Eisbären (*Ursus maritimus*). *Säugetierkundliche Mitteilungen* **9**, 12–15.
- DITTRICH, L. & KRONBERGER, H. (1963). Biologisch-anatomische Untersuchungen über die Fortpflanzungsbiologie des Braunbären (*Ursus arctos* L.) und anderen Ursiden in Gefangenschaft. *Zeitschrift für Säugetierkunde* **28**, 129–155.
- DIXON, A. F. (1987). Observations on the evolution of the genitalia and copulatory behaviour in male primates. *Journal of Zoology* **213**, 423–443.
- DRUECKER, J. D. (1972). *Aspects of reproduction in Myotis volans, Lasionycteris noctivagans, and Lasius cinereus*. PhD Thesis: University of New Mexico.
- EADIE, W. R. & HAMILTON, W. J. (1958). Reproduction of the fisher in New York. *New York Fish and Game Journal* **5**, 77–83.
- EALEY, E. H. M. (1963). The ecological significance of delayed implantation in a population of the hill kangaroo (*Macropus robustus*). In *Delayed Implantation* (ed. A. C. ENDERS), pp. 33–48. The University of Chicago Press, Chicago.
- EBERHARD, W. G. (1985). *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge.
- EBERHARD, W. G. (1996). *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton.
- EDWARDS, R. (1993). Entomological and mammalogical perspectives on genital differentiation. *Trends in Ecology & Evolution* **8**, 406–409.
- ENDERS, R. K. (1952). Reproduction in the mink (*Mustela vison*). *Proceedings of the American Philosophical Society* **96**, 691–755.
- ENDERS, A. C. (1966). The reproductive cycle of the nine-banded armadillo (*Dasypus novemcinctus*). *Symposia of the Zoological Society of London* **15**, 295–310.
- ENDERS, R. K. & PEARSON, O. P. (1943). The blastocyst of the fisher. *Anatomical Record* **85**, 285–287.
- EVANS, J. P., PIEROTTI, M. & PILASTRO, A. (2003). Male mating behavior and ejaculate expenditure under sperm competition risk in the eastern mosquitofish. *Behavioral Ecology* **14**, 268–273.
- EWERT, M. A. (1992). Cold torpor, diapause, delayed hatching and aestivation in reptiles and birds. In *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles* (eds D. C. DEEMING and M. W. J. FERGUSON), pp. 173–191. Cambridge University Press, Cambridge.
- EWER, R. F. & WEMMER, C. (1974). The behaviour in captivity of the African civet, *Civettictis civetta* (Schreber). *Zeitschrift für Tierpsychologie* **34**, 359–394.
- FAY, F. H. (1981). Walrus—*Odobenus rosmarus*. In *Handbook of Marine Mammals* (Volume I, eds S. H. RIDGWAY and R. H. HARRISON), pp. 1–23. Academic Press, London.
- FAY, F. H. (1982). *Ecology and Biology of the Pacific Walrus Odobenus Rosmarus Divergens*. Illiger. U.S. Fish and Wildlife Service, Washington.
- FENTON, M. B. (1984). Sperm competition? The case of Vespertilionid and Rhinolophid bats. In *Sperm Competition and the Evolution of Animal Mating Systems* (ed. R. L. SMITH), pp. 573–585. Academic Press, London.
- FERGUSON, S. H., HIGDON, J. W. & LARIVIÈRE, S. (2006). Does seasonality explain the evolution and maintenance of delayed implantation in the family Mustelidae (Mammalia: Carnivora)? *Oikos* **114**, 249–256.
- FERGUSON, S. H. & LARIVIÈRE, S. (2004). Are long penis bones an adaptation to high latitude snowy environments? *Oikos* **105**, 255–267.
- FERGUSON, S. H., VIRGL, J. A. & LARIVIÈRE, S. (1996). Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores. *Ecoscience* **3**, 7–17.
- FISHER, H. C. (1954). Delayed implantation in the harbour seal, *Phoca vitulina* L. *Nature* **173**, 879–880.

- FLEMING, T. H. (1971). *Artibeus jamaicensis*: delayed embryonic development in a neotropical bat. *Science* **171**, 402–404.
- FLEMING, D., CINDERERY, R. N. & HEARN, J. P. (1983). The reproductive biology of Bennett's wallaby (*Macropus rufogriseus rufogriseus*) ranging free at Whipsnade Park. *Journal of Zoology* **201**, 283–291.
- FLYNN, T. T. (1930). The uterine cycle of pregnancy and pseudopregnancy as it is in the diprotodont marsupial *Bettongia cuniculus* with notes on the reproductive phenomena in this marsupial. *Transactions of the Linnaean Society of New South Wales* **55**, 506–531.
- FOX, S., SPENCER, H. & O'BRIEN, G. M. (2008). Analysis of twinning in flying-foxes (Megachiroptera) reveals superfecundation and multiple-paternity. *Acta Chiropterologica* **10**, 271–278.
- FRIES, S. (1880). Über die Fortpflanzung von *Meles taxus*. *Zoologische Anzeiger* **3**, 486–492.
- FROST, K. J. & LOWRY, L. F. (1981). Ringed, Baikal, and Caspian seals—*Phoca hispida*, *Phoca sibirica* and *Phoca caspica*. In *Handbook of Marine Mammals* (Volume II, eds S. H. RIDGEWAY and R. J. HARRISON), pp. 29–53. Academic Press, London.
- GAGE, M. J. G. (1998). Mammalian sperm morphology. *Proceedings of the Royal Society of London Series B: Biological Sciences* **265**, 97–103.
- GALLUP, G. G. & BURCH, R. L. (2004). Semen displacement as a sperm competition strategy in humans. *Evolutionary Psychology* **2**, 12–23.
- GATES, W. H. (1936). Keeping bats in captivity. *Journal of Mammalogy* **17**, 268–272.
- GILMORE, D. P. (1969). Seasonal reproductive periodicity in the male Australian Brush-tailed possum (*Trichosurus vulpecula*). *Journal of Zoology, London* **157**, 75–98.
- GINSBERG, J. R. & RUBENSTEIN, D. I. (1990). Sperm competition and variation in zebra mating behavior. *Behavioral Ecology and Sociobiology* **26**, 427–434.
- GOMENDIO, M. & ROLDAN, E. R. S. (1993). Coevolution between male ejaculates and female reproductive biology in eutherian mammals. *Proceedings of the Royal Society of London Series B: Biological Sciences* **252**, 7–12.
- GOPALAKRISHNA, A. (1949). Studies on the embryology of the Microchiroptera, Part III. The histological changes in the genital organs and accessory reproductive structures during the sex cycle of the vespertilionid bat, *Scotophilus wroughtoni* (Thomas). *Proceedings of the Indian Academy of Science* **30**, 17–49.
- GREENSIDES, R. D. & MEAD, R. A. (1973). Ovulation in the spotted skunk (*Spilogale putorius latifrons*). *Biology of Reproduction* **8**, 576–584.
- GUTHRIE, M. J. (1933). The reproductive cycles of some cave bats. *Journal of Mammalogy* **14**, 199–216.
- HAMILTON, J. E. (1939). A second report on the southern sea lion, *Otaria byronia* (de Blainville). *Discovery Reports* **19**, 121–164.
- HAMILTON, W. J. & EADIE, W. R. (1964). Reproduction in the otter, *Lutra canadensis*. *Journal of Mammalogy* **45**, 242–252.
- HAMLETT, G. W. D. (1932a). Observations on the embryology of the badger. *Anatomical Record* **53**, 283–303.
- HAMLETT, G. W. D. (1932b). The reproductive cycle in the armadillo. *Zeitschrift für Wissenschaft Zoologie* **141**, 143–157.
- HAMLETT, G. W. D. (1935). Delayed implantation and discontinuous development in the mammals. *Quarterly Review of Biology* **10**, 432–447.
- HANSSON, A. (1947). The physiology of reproduction in the mink (*Mustela vison*, Schreb.) with special reference to delayed implantation. *Acta Zoologica* **28**, 1–447.
- HARCOURT, A. H., HARVEY, P. H., LARSON, S. G. & SHORT, R. V. (1981). Testes weight, body weight and breeding system in primates. *Nature* **293**, 55–57.
- HARRISON, R. J. (1963). A comparison of factors involved in delayed implantation in badgers and seals in Great Britain. In *Delayed Implantation* (ed. A. C. ENDERS), pp. 99–114. University of Chicago Press, Chicago.
- HARRISON, R. J. (1969). Reproduction and reproductive organs. In *The Biology of Marine Mammals* (ed. T. H. ANDERSEN), pp. 253–348. Academic Press, London.
- HARRISON, R. J., MATTHEWS, L. H. & ROBERTS, J. M. (1952). Reproduction in some Pinnipedia. *Transactions of the Zoological Society of London* **27**, 437–540.
- HARTMAN, C. G. (1923). The oestrous cycle of the opossum. *American Journal of Anatomy* **32**, 353–421.
- HAYSSEN, V., VAN TIENHOVEN, A. & VAN TIENHOVEN, A. (1993). *Asdell's Patterns of Mammalian Reproduction*. Comstock Publishing Associates, Ithaca.
- HEIDEMAN, P. D. (1988). The timing of reproduction in the fruit bat *Haplonycteris fischeri* (Pteropodidae): geographic variation and delayed development. *Journal of Zoology, London* **215**, 577–595.
- HEIDEMAN, P. D. (1989). Delayed development in Fischer's pygmy fruit bat, *Haplonycteris fischeri*, in the Philippines. *Journal of Reproduction and Fertility* **85**, 363–382.
- HEIDEMAN, P. D., CUMMINGS, J. A. & HEANEY, L. R. (1993). Reproductive timing and early embryonic development in an Old World fruit bat, *Otopterus cartilagonodus* (Megachiroptera). *Journal of Mammalogy* **74**, 621–630.
- HEIDEMAN, P. D. & POWELL, K. S. (1998). Age-specific reproductive strategies and delayed embryonic development in an old world fruit bat, *Ptenochirus jagori*. *Journal of Mammalogy* **79**, 295–311.
- HEWER, H. R. & BACKHOUSE, K. M. (1968). Embryology and foetal growth of the grey seal, *Halichoerus grypus*. *Journal of Zoology, London* **155**, 507–533.
- HIGGINSON, D. M., MILLER, K. B., SEGRAVES, K. A. & PITNICK, S. (2012). Female reproductive tract form drives the evolution of complex sperm morphology. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 4538–4543.
- HIRAIWA, Y. K. & UCHIDA, T. (1956). Fertilization capacity of spermatozoa stored in the uterus after copulation in the fall. *Science Bulletin of the Faculty of Agriculture Kyushu University* **31**, 565–574.
- HOGG, J. T. (1988). Copulatory tactics in relation to sperm competition in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology* **22**, 49–59.
- HOLLAND, O. J. & GLEESON, D. M. (2005). Genetic characterization of blastocysts and the identification of multiple paternity in the stoat (*Mustela erminea*). *Conservation Genetics* **6**, 855–858.
- HOLT, W. V. (2011). Mechanisms of sperm storage in the female reproductive tract: an interspecies comparison. *Reproduction in Domestic Animals* **46**, 68–74.
- HOOD, C. S. & SMITH, J. D. (1989). Sperm storage in a tropical nectar-feeding bat, *Macroglossus minimus* (Pteropodidae). *Journal of Mammalogy* **70**, 404–406.
- HOSKEN, D. J. (1997). Sperm competition in bats. *Proceedings of the Royal Society of London Series B: Biological Sciences* **264**, 385–392.
- HOSKEN, D. J. (1998). Sperm fertility and skewed paternity during sperm competition in the Australian long-eared bat *Nyctophilus geoffroyi* (Chiroptera: Vespertilionidae). *Journal of Zoology, London* **245**, 93–100.
- HOSKEN, D. J., JONES, K. E., CHIPPERFIELD, K. & DIXSON, A. (2001). Is the bat penis sexually selected? *Behavioral Ecology and Sociobiology* **50**, 450–460.
- HOSKEN, D. J. & STOCKLEY, P. (2004). Sexual selection and genital evolution. *Trends in Ecology & Evolution* **19**, 87–93.
- HUGHES, R. L. (1962a). Reproduction in the macropod marsupial *Potorous tridactylus* (Kerr). *Australian Journal of Zoology* **10**, 193–224.
- HUGHES, R. L. (1962b). Role of the corpus luteum in marsupial reproduction. *Nature* **194**, 890–891.
- IMMLER, S., MOORE, H. D. M., BREED, W. G. & BIRKHEAD, T. R. (2007). By hook or by crook? Morphometry, competition and cooperation in rodent sperm. *PLoS ONE* **2**, e170.
- ISAKOVA, G. K. (2006). The biological significance of the phenomenon of delayed implantation in mammals from the viewpoint of a cytogeneticist. *Doklady Biological Sciences* **409**, 349–350.
- JACOME, L. & PARERA, A. (1995). Neotropical river otter, *Lutra longicaudis*, breeding under captive conditions in Buenos Aires Zoo, Argentina. *International Union for the Conservation of Nature, Otter Specialist Group Bulletin* **12**, 34–36.
- JEULIN, C. & SOUFIR, J. C. (1992). Reversible intracellular ATP changes in intact rat spermatozoa 411 and effects on flagellar sperm movement. *Cell Motility and the Cytoskeleton* **21**, 210–222.
- JUDIN, B. S. (1974). Reproduction of *Asioscalops altaica* Nikolsky, 1883. *Acta Theriologica* **19**, 355–366.
- KEELEY, A. T. H. & KEELEY, B. W. (2004). The mating system of *Tadarida brasiliensis* (Chiroptera: Molossidae) in a large highway bridge colony. *Journal of Mammalogy* **85**, 113–119.
- KENAGY, G. J. & TROMBULAK, S. C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy* **67**, 1–22.
- KING, H. D. (1913). Some anomalies in the gestation of the albino rat (*Mus norvegicus albinus*). *Biological Bulletin* **24**, 377–391.
- KING, L. M., BRILLARD, J. P., GARRETT, W. M., BAKST, M. R. & DONOGHUE, A. M. (2002). Segregation of spermatozoa within sperm storage tubules of fowl and turkey hens. *Reproduction* **123**, 79–86.
- KIRKPATRICK, T. H. (1965). Studies of the Macropodidae in Queensland. 3. Reproduction in the grey kangaroo (*Macropus major*) in southern Queensland. *Queensland Journal of Agricultural and Animal Sciences* **22**, 319–328.
- KITCHNER, D. J. (1975). Reproduction in female Gould's wattled bat *Chalinolobus gouldii* (Gray) (Vespertilionidae) in Western Australia. *Australian Journal of Zoology* **23**, 29–42.
- KLEVEN, O., FOSSOY, F., LASKEMOEN, T., ROBERTSON, R. J., RUDOLFSEN, G. & LIEJELD, J. T. (2009). Comparative evidence for the evolution of sperm swimming speed by sperm competition and female sperm storage duration in passerine birds. *Evolution* **63**, 2466–2473.
- KOFRON, C. P. (1997). Reproduction in two species of congeneric fruit bats (*Cynopterus*) in Bruni, Borneo. *Journal of Zoology* **243**, 485–506.
- KOLB, A. (1950). Beiträge zur biologie einheimischer Fledermause. *Zoologische Jahrbucher Abteilung für Systematische Geographie der Tiere* **78**, 547–573.
- KONARZEWSKI, M. (1993). The evolution of clutch size and hatching asynchrony in altricial birds: the effect of environmental variability, egg failure and predation. *Oikos* **67**, 97–106.
- KOOSMAN, G. L. (1981). Weddell seal – *Leptonychotes weddelli*. In *Handbook of Marine Mammals* (Volume II, eds S. H. RIDGEWAY and R. J. HARRISON), pp. 275–296. Academic Press, London.
- KOVACS, K. M. & LAVIGNE, D. M. (1986). *Cystophora cristata*. *Mammalian Species* **258**, 1–9.
- KOZHOV, M. (1947). *Lake Baikal and Its life*. Dr. W. Junk Publishers, The Hague.
- KRISHNA, A. (1997). Adiposity and androstenedione production in relation to delayed ovulation in the Indian bat, *Scotophilus heathi* – animal models. *Comparative Biochemistry and Physiology* **116**, 97–101.
- KRISHNA, A. (1999). Reproductive delays in Chiropterans. In *Comparative Endocrinology and Reproduction* (eds K. P. JOY, A. KRISHNA and C. HALDAR), pp. 410–421. Narosa Publishing House, New Delhi.

- KRISHNA, A. & DOMINIC, C. J. (1982). Differential rates of fetal growth in two successive pregnancies in the emballonurid bat, *Taphozous longimanus* Hardwicke. *Biology of Reproduction* **27**, 351–353.
- KRUTZSCH, P. H. (1975). Reproduction of the Canyon bat, *Pipistrellus hesperus*, in Southwestern United States. *American Journal of Anatomy* **143**, 163–200.
- KRUTZSCH, P. H., CRICHTON, E. G. & NAGLE, R. B. (1982). Studies on prolonged spermatozoa survival in Chiroptera: a morphological examination of storage and clearance of intrauterine and cauda epididymal spermatozoa in the bats *Myotis lucifugus* and *M. velifer*. *American Journal of Anatomy* **165**, 421–434.
- KURTA, A. & KUNZ, T. H. (1987). Size of bats at birth and maternal investment during pregnancy. *Symposium of the Zoological Society of London* **57**, 79–106.
- KURTA, A. & LEHR, G. C. (1995). *Lasiurus ega*. *Mammalian Species* **515**, 1–7.
- LARIVIÈRE, S. & FERGUSON, S. H. (2003). Evolution of induced ovulation in North American carnivores. *Journal of Mammalogy* **84**, 937–947.
- LARIVIÈRE, S. & PASITSCHNIK-ARTS, M. (1996). *Vulpes vulpes*. *Mammalian Species* **537**, 1–11.
- LAURIE, A. & SEIDENSTICKER, J. (1977). Behavioural ecology of the Sloth bear (*Melursus ursinus*). *Journal of Zoology, London* **182**, 187–204.
- LAWS, R. M. (1956). The elephant seal (*Mirounga leonina* Linn.) III The physiology of reproduction. *Falkland Islands Dependencies Survey Scientific Report* **15**, 1–66.
- LAWS, R. M., BAIRD, A. & BRYDEN, M. M. (2003). Breeding season and embryonic diapause in crab-eater seals (*Lobodon carcinophagus*). *Reproduction* **126**, 365–370.
- LEMAÎTRE, J. F., RAMM, S., HURST, J. L. & STOCKLEY, P. (2011). Social cues of sperm competition influence accessory reproductive gland size in a promiscuous mammal. *Proceedings of the Royal Society of London Series B: Biological Sciences* **278**, 1171–1176.
- LINDENFORS, P., DALEN, L. & ANGERBJOERN, A. (2003). The monophyletic origin of delayed implantation in carnivores and its implications. *Evolution* **57**, 1952–1956.
- LOYD, J. A. & CHRISTIAN, J. T. (1969). Reproductive activity of individual females in three experimental freely growing populations of house mice (*Mus musculus*). *Journal of Mammalogy* **50**, 49–59.
- LOYD, S., HALL, L. & BRADLEY, A. J. (1999). Reproductive strategies of a warm temperate vespertilionid, the large-footed myotis, *Myotis moluccarum* (Microchiroptera: Vespertilionidae). *Australian Journal of Zoology* **43**, 261–274.
- LUDLOW, A. M. & MAGURRAN, A. E. (2006). Gametic isolation in guppies (*Poecilia reticulata*). *Proceedings of the Royal Society of London Series B: Biological Sciences* **273**, 2477–2482.
- LÜPOLD, S. (2013). Ejaculate quality and constraints in relation to sperm competition levels among Eutherian mammals. *Evolution* **67**, 3052–3060.
- LÜPOLD, S., McELLIOTT, A. G. & HOSKEN, D. J. (2004). Bat genitalia: allometry, variation and good genes. *Biological Journal of the Linnean Society* **83**, 497–507.
- LUPPI, P. (2003). How immune mechanisms are affected by pregnancy. *Vaccine* **21**, 3352–3357.
- MACDONALD, D. (1984). *The Encyclopedia of Mammals*. Facts on File Publications, New York.
- MANSFIELD, A. W. (1958). The breeding and reproductive cycle of the Weddell seal (*Leptonychotes weddelli*, Lesson). *Falkland Island Dependencies Survey, Scientific Report* **18**, 1–41.
- MARLOW, B. J. (1961). Reproductive behaviour of the marsupial mouse, *Antechinus flavipes* (Waterhouse) (Marsupialia) and the development of the pouch young. *Australian Journal of Zoology* **9**, 203–410.
- MATTHEWS, L. H. (1937). Female cycle in the British horseshoe bats *Rhinolophus ferrumequinum insulanus* Barrett-Hamilton and *R. hipposideros minutus* Montagu. *Transactions of the Zoological Society of London* **23**, 244–266.
- MATTHEWS, L. H. (1942). Notes on the genitalia and reproduction of some African bats. *Journal of Zoology* **111**, 289–346.
- MAYNES, G. M. (1973). Reproduction in the Parma wallaby, *Macropus parma* (Waterhouse). *Australian Journal of Zoology* **21**, 331–351.
- MCCUSKER, J. S. (1974). Breeding Malayan sun bears at Forth Worth Zoo. *International Zoo Yearbook* **15**, 118–119.
- MCLAREN, I. A. (1958). Some aspects of growth and reproduction of the bearded seal, *Erignathus barbatus* (Erxleben). *Journal of the Fisheries Research Board of Canada* **15**, 219–227.
- MCLAREN, A. (1968). A study of blastocysts during delay and subsequent implantation in lactating mice. *Journal of Endocrinology* **42**, 453–463.
- MEAD, R. A. (1968a). Reproduction in eastern forms of the spotted skunk (genus *Spilogale*). *Journal of Zoology* **156**, 119–136.
- MEAD, R. A. (1968b). Reproduction in western forms of the spotted skunk (genus *Spilogale*). *Journal of Mammalogy* **49**, 373–390.
- MEAD, R. A. (1981). Delayed implantation in the Mustelidae with special emphasis on the spotted skunk. *Journal of Reproduction and Fertility, Supplement* **29**, 11–24.
- MEAD, R. A. (1989). The physiology and evolution of delayed implantation in carnivores. In *Carnivore Behavior, Ecology, and Evolution* (ed. J. L. GITTLEMAN), pp. 437–464. Comstock Publishing Associates, Ithaca.
- MEAD, R. A. (1993). Embryonic diapause in vertebrates. *Journal of Experimental Biology* **266**, 629–641.
- MEDWAY, F. L. S. (1972). Reproductive cycles of the flat-headed bats *Tylonycteris pachypus* and *T. robustula* (Chiroptera: Vespertilioninae) in a humid equatorial environment. *Zoological Journal of the Linnean Society* **51**, 33–61.
- MEENAKUMARI, K. J. & KRISHNA, A. (2005). Delayed embryonic development in the Indian short-nosed fruit bat, *Cynopterus sphinx*. *Zoology* **108**, 131–140.
- MENDELSSOHN, H., BEN-DAVID, M. & HELLWING, S. (1988). Reproduction and growth of the marbled polecat (*Vormela peregusna syriaca*) in Israel. *Journal of Reproduction and Fertility, Abstract Series* **1**, 20.
- MERCHANT, J. C. (1976). Breeding biology of the agile wallaby, *Macropus agilis* (Gould) (Marsupialia: Macropodidae), in captivity. *Australian Wildlife Research* **3**, 93–103.
- MERCHANT, J. C. & CALABY, J. H. (1981). Reproductive biology of the red-necked wallaby (*Macropus rufogriseus banksianus*) and Bennett's wallaby (*M. r. rufogriseus*) in captivity. *Journal of Zoology* **194**, 203–217.
- MEREDITH, R. W., JANECKA, J. E., GATESY, J., RYDER, O. A., FISHER, C. A., TEELING, E. C., GOODBLA, A., EIZIRIK, E., SIMÃO, T. L. L., STADLER, T., RABOSKY, D. L., HONEYCUTT, R. L., FLYNN, J. J., INGRAM, C. M., STEINER, C., WILLIAMS, T. L., ROBINSON, T. J., BURK-HERRICK, A., WEWSTERMAN, M., AYOUB, N. A., SPRINGER, M. S. & MURPHY, W. J. (2011). Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* **334**, 521–524.
- VAN DER MERWE, M. (1978). Delayed implantation in the Natal Clinging Bat *Miniopterus schreibersii natalensis* (A. Smith, 1834). In *Proceedings of the 5th International Bat Research Conference* (eds D. E. WILSON and A. L. GARDNER), pp. 113–123. Texas Tech Press, Lubbock.
- VAN DER MERWE, M. & RAUTENBACH, I. L. (1990). Reproduction in the rusty bat, *Pipistrellus rusticus*, in the northern Transvaal bushveld, South Africa. *Journal of Reproduction and Fertility* **89**, 537–542.
- MILLER, E. H. & BURTON, L. E. (2001). It's all relative: allometry and variation in the baculum (os penis) of the harp seal, *Pagophilus groenlandicus* (Carnivora: Phocidae). *Biological Journal of the Linnean Society* **72**, 345–355.
- MILLER-BUTTERWORTH, C. M., MURPHY, W. J., O'BRIEN, S. J., JACOBS, D. S., SPRINGER, M. S. & TEELING, E. C. (2007). A family matter: conclusive resolution of the taxonomic position of the long-fingered bats, *Miniopterus*. *Molecular Biology and Evolution* **24**, 1553–1561.
- MITCHELL, G. C. (1965). *A natural history study of the funnel-eared bat Natalus stramineus*. Masters Thesis: University of Arizona.
- MİYAMOTO, H. & CHANG, M. C. (1972). Fertilization in vitro of mouse and hamster eggs after the removal of follicular cells. *Journal of Reproduction and Fertility* **30**, 309–312.
- MONTOTO, L. G., MAGAN, C., TOURMENTE, M., MARTÍN-COELLO, J., CRESPO, C., LUQUE-LARENA, J. J., GOMENDIO, M. & ROLDAN, E. R. S. (2011). Sperm competition, sperm numbers and sperm quality in murid rodents. *PLoS ONE* **6**, e18173.
- MORI, T. & UCHIDA, T. A. (1980). Sperm storage in the reproductive tract of the female Japanese long-fingered bat, *Miniopterus schreibersii fuliginosus*. *Journal of Reproduction and Fertility* **58**, 429–433.
- MURPHY, R. C. & NICHOLS, J. T. (1913). Long Island fauna and flora - I. the bats (Order Chiroptera). *Science Bulletin of the Museum, Brooklyn Institute of Arts and Sciences* **2**, 1–15.
- MYERS, P. (1977). Patterns of reproduction of four species of vespertilionid bats in Paraguay. *University of California Publications in Zoology* **107**, 1–41.
- NEAL, E. G. & HARRISON, R. J. (1958). Reproduction in the European badger (*Meles meles* L.). *Transactions of the Zoological Society of London* **29**, 67–130.
- NOVIKOV, G. A. (1956). *Carnivorous Mammals of the Fauna of the USSR*. Israel Program for Scientific Translations, Jerusalem.
- NOWAK, R. M. & PARADISO, J. L. (1983). *Walker's Mammals of the World*. Johns Hopkins, Baltimore.
- NYAKATURA, K. & BININDA-EMONDS, O. R. P. (2012). Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* **10**, 12.
- OATES, J. E., BRADSHAW, F. J., BRADSHAW, S. D., STEAD-RICHARDSON, E. J. & PHILIPPE, D. L. (2007). Reproduction and embryonic diapause in a marsupial: insights from captive female Honey possums, *Tarsipes rostratus* (Tarsipedidae). *General and Comparative Endocrinology* **150**, 445–461.
- ODELL, D. K. (1981). California sea lion - *Zalophus californicanus*. In *Handbook of Marine Mammals* (Volume I, eds S. H. RIDGEWAY and R. J. HARRISON), pp. 67–97. Academic Press, London.
- OLSSON, M., MADSEN, T. & SHINE, R. (1997). Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proceedings of the Royal Society of London Series B: Biological Sciences* **264**, 455–459.
- ORR, T. J. (2012). *Delayed implantation in the Carnivora: causes and consequences*. PhD Thesis: University of California, Riverside.
- ORR, T. J. & ZUK, M. (2012). Sperm storage quick guide. *Current Biology* **22**(1), R8–R10.
- ORR, T. J. & ZUK, M. (2013). Do reproductive delays facilitate sperm competition in bats? *Behavioral Ecology and Sociobiology* **67**, 1903–1913 (doi: 10.1007/s00265-013-1598-2).
- ØRTISLAND, T. (1964). Klappmysshunnens fortplaningsbiologi. *Fisken Havet* **1**, 1–15.
- ONBERRY, B. A. (1979). Female reproductive patterns in hibernating bats. *Journal of Reproduction and Fertility* **56**, 359–367.
- PAGENSTECHE, H. A. (1859). Über die Begattung von *Vesperugo pipistrellus*. *Verhandlungen des Naturhistorisch-medizinischen Vereins zu Heidelberg* **1**, 194–195.

- PARKER, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* **45**, 525–567.
- PARKER, P. (1977). An ecological comparison of marsupial and placental patterns of reproduction. In *The Biology of Marsupials* (eds B. STONEHOUSE and D. GILMORE), pp. 273–286. Macmillan, London.
- PARKER, C. (1979). Birth, care and development of Chinese hog badgers. *International Zoo Yearbook* **19**, 182–185.
- PARKER, G. A. (1984). Sperm competition and the evolution of animal mating strategies. In *Sperm Competition and the Evolution of Animal Mating Systems* (ed. R. L. SMITH), pp. 1–60. Academic Press, London.
- PARKER, G. A. (1990). Sperm competition games: raffles and roles. *Proceedings of the Royal Society of London Series B: Biological Sciences* **242**, 120–126.
- PEARSON, O. P. & ENDERS, R. K. (1944). Duration of pregnancy in certain mustelids. *Journal of Experimental Zoology* **95**, 21–35.
- PEARSON, O. P., KOFORD, M. R. & PEARSON, A. K. (1952). Reproduction of the lump-nosed bat (*Corynorhinus rafinesquii*) in California. *Journal of Mammalogy* **33**, 273–320.
- PERCHEG, G., JEULIN, C., COSSON, J., ANDRÉ, F. & BILLARD, R. (1995). Relationship between sperm ATP content and motility of carp spermatozoa. *Journal of Cell Science* **108**, 747–753.
- PETRI, B., PAABO, S., VON HAESLER, A. & TAUTZ, D. (1997). Paternity assessment and population subdivision in a natural population of the larger mouse-eared bat *Myotis myotis*. *Molecular Ecology* **6**, 235–242.
- PHILLIPS, W. R. & INWARDS, S. J. (1985). The annual activity and breeding cycles of Gould's Long-eared Bat, *Nyctophilus gouldi* (Microchiroptera: Vespertilionidae). *Australian Journal of Zoology* **33**, 111–126.
- PITNICK, S., HOSKEN, D. J. & BIRKHEAD, T. R. (2009). Sperm morphological diversity. In *Sperm Biology: An Evolutionary Perspective* (eds T. R. BIRKHEAD, D. J. HOSKEN and S. PITNICK), pp. 69–149. Academic Press, London.
- PITNICK, S., MARKOW, T. & SPICER, G. S. (1999). Evolution of multiple kinds of female sperm-storage organs in *Drosophila*. *Evolution* **53**, 1804–1822.
- POOLE, W. E. (1975). Reproduction in the two species of grey kangaroos, *Macropus giganteus* (Shaw), and *M. fuliginosus* (Desmarest). II. Gestation parturition and pouch life. *Australian Journal of Zoology* **23**, 333–353.
- POOLE, W. E. & CATLING, P. C. (1974). Reproduction in the two species of grey kangaroos, *Macropus giganteus* and *M. fuliginosus* (Desmarest). I. Sexual maturity and oestrus. *Australian Journal of Zoology* **22**, 277–302.
- PRELL, H. (1927). Über doppelte Brunstzeit und verlängerte Tragzeit bei den einheimischen Arten der Mardergattung Martes Pincl. *Zoologische Anzeiger* **74**, 122–128.
- PTAK, G., TACCONI, E., CZERNIK, M., TOSCHI, P., MODLINSKI, J. A. & LOI, P. (2012). Embryonic diapause is conserved across mammals. *PLoS ONE* **7**, E33027.
- PUSCHMAN, W., SCHUPPEL, K. F. & KRONBERGER, H. (1977). Detection of blastocyst in uterine lumen of Indian bear *Melursus u. ursinus*. In *Sickness in Zoos* (eds R. IPPEN and H. D. SCHRADER), pp. 389–391. Akademie Verlag, Berlin.
- RACEY, P. A. (1973a). The reproductive cycle in male noctule bats, *Nyctalus noctula*. *Journal of Reproduction and Fertility* **41**, 169–182.
- RACEY, P. A. (1973b). The viability of spermatozoa after prolonged sperm storage by male and female European bats. *Periodicum Biologorum* **75**, 201–205.
- RACEY, P. A. (1975). The prolonged survival of spermatozoa in bats. In *The Biology of the Male Gamete* (eds J. G. DUCKETT and P. A. RACEY), pp. 385–416. Academic Press, London.
- RACEY, P. A. (1979). The prolonged storage and survival of spermatozoa in Chiroptera. *Journal of Reproduction and Fertility* **56**, 391–402.
- RACEY, P. A. (1982). Ecology of bat reproduction. In *Ecology of Bats* (ed. T. H. KUNZ), pp. 57–104. Plenum Press, New York.
- RACEY, P. A. & ENTWISTLE, A. C. (2000). Life-history and reproductive strategies of bats. In *Reproductive Biology of Bats* (eds E. G. CRICHTON and P. H. KRUTZSCH), pp. 363–414. Academic Press, London.
- RACEY, P. A. & POTTS, D. M. (1970). Relationship between stored spermatozoa and the uterine epithelium in the pipistrelle bat (*Pipistrellus pipistrellus*). *Journal of Reproduction and Fertility* **22**, 57–63.
- RAMAKRISHNA, P. A. & RAO, K. V. B. (1977). Reproductive adaptations in the Indian rhinolophid bat, *Rhinolophus rouxi* (Temminck). *Current Science* **46**, 270–271.
- RAMM, S. A., OLIVER, P., PONTING, C. P., STOCKLEY, P. & EMES, R. D. (2008). Sexual selection and the adaptive evolution of mammalian ejaculate proteins. *Molecular Biology and Evolution* **25**, 207–219.
- RAMM, S. A., PARKER, G. A. & STOCKLEY, P. (2005). Sperm competition and the evolution of male reproductive anatomy in rodents. *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**, 949–955.
- RASWEILER, J. J. (1977). Preimplantation development, fate of zona pellucida, and observations on the glycogen-rich oviduct of the little bulldog bat, *Noctilio albiventris*. *American Journal of Anatomy* **150**, 269–300.
- RASWEILER, J. J. (1979). Early embryonic development and implantation in bats. *Journal of Reproduction and Fertility* **56**, 403–416.
- RASWEILER, J. J. (1987). Prolonged receptivity to the male and the fate of spermatozoa in the female black mastiff bat *Molossus ater*. *Journal of Reproduction and Fertility* **79**, 643–654.
- RASWEILER, J. J. & BADWAIK, N. K. (1997). Delayed development in the short-tailed fruit bat, *Carollia perspicillata*. *Journal of Reproduction and Fertility* **109**, 7–20.
- RAUSCH, R. A. & PEARSON, A. M. (1972). Notes on the Wolverine in Alaska and the Yukon Territory. *Journal of Wildlife Management* **36**, 249–268.
- REEVES, R. R. & LING, J. K. (1981). Hooded seal. In *Handbook of Marine Mammals* (eds S. H. RIDGEWAY and R. J. HARRISON), pp. 1–359. Academic Press, London.
- RENFREE, M. B. (1979). Initiation of development of diapausing embryo by mammary denervation during lactation in a marsupial. *Nature* **278**, 549–551.
- RENFREE, M. B. (1980). Embryonic diapause in the honey possum, *Tarsipes spencerae*. *Search* **11**, 81.
- RENFREE, M. B. (1994). Endocrinology of pregnancy, parturition, and lactation in marsupials. In *Marshall's Physiology of Reproduction: Pregnancy and Lactation* (Volume III, ed. G. LAMING), pp. 677–766. Chapman & Hall, London.
- RENFREE, M. B. & CALABY, J. H. (1981). Background to delayed implantation and embryonic diapause. *Journal of Reproduction and Fertility* **29**, 1–9.
- RENFREE, M. B. & SHAW, G. (2000). Diapause. *Annual Review of Physiology* **62**, 353–375.
- RETZIUS, G. (1900). Zur Kenntnis der Entwicklungsgeschichte des Renntieres und des Rehes. *Biologische Untersuchungen* **9**, 65–66.
- RICE, D. W. (1957). Life history and ecology of *Myotis austroriparius* in Florida. *Journal of Mammalogy* **38**, 15–32.
- RIEDMAN, M. (1990). *The Pinnipeds: Seals, Sea Lions, and Walrus*. University of California Press, Berkeley.
- RIJSELAERE, T., VAN SOOM, A., VAN CRUCHTEN, S., CORYN, M., GÖRTZ, K., MAES, D. & DE KRUIF, A. (2004). Sperm distribution in the genital tract of the bitch following artificial insemination in relation to the time of ovulation. *Reproduction* **128**, 801–911.
- ROBERTS, T. J. (1977). *The Mammals of Pakistan*. Ernst Benn, London.
- ROBERTS, M. S. & GITTLEMAN, J. L. (1984). *Ailurus fulgens*. *Mammalian Species* **222**, 1–8.
- ROELLIG, K., MENZIES, B. R., HILDEBRANDT, T. B. & BOERTZ, F. (2011). The concept of superfetation: a critical review on a 'myth' in mammalian reproduction. *Biological Reviews* **86**, 77–95.
- ROSE, R. W. (1978). Reproduction and evolution in female Macropodidae. *Australian Mammalogy* **2**, 65–72.
- ROSE, R. W. & MCCARTNEY, D. J. (1982). Reproduction of the red-bellied pademelon, *Thylogale billardieri* (Marsupialia). *Australian Wildlife Research* **9**, 27–32.
- ROSEVEAR, D. R. (1974). *The Carnivores of West Africa*. British Museum of Natural History, London.
- ROTH, T. L., HOWARD, J. C., DONOGHUE, A. M., SWANSON, W. F. & WILDT, D. E. (1994). Function and culture requirements of snow leopard (*Panthera unica*) spermatozoa in vitro. *Journal of Reproduction and Fertility* **101**, 563–569.
- RYAN, J. M. (1991). Morphology of the glans penis in four genera of molossid bats (Chiroptera: Molossidae). *Journal of Mammalogy* **72**, 658–668.
- SANDELL, M. (1990). The evolution of seasonal delayed implantation. *Quarterly Review of Biology* **65**, 23–42.
- SCHUSTERMAN, R. J. (1981). Steller sea lion - *Eumetopias jubatus*. In *Handbook of Marine Mammals* (Volume I, eds S. H. RIDGEWAY and R. J. HARRISON), pp. 119–141. Academic Press, London.
- SCOTT, M. A. (2000). A glimpse at sperm function in vivo: sperm transport and epithelia interaction in the female reproductive tract. *Animal Reproduction Science* **60–61**, 337–348.
- SCRIMSHAW, N. S. (1944). Superfetation in Poeciliid fishes. *Copeia* **3**, 180–183.
- SHARMAN, G. B. (1955a). Studies on marsupial reproduction. II. The oestrous cycle of *Setonix brachyurus*. *Australian Journal of Zoology* **3**, 44–55.
- SHARMAN, G. B. (1955b). Studies on marsupial reproduction. IV. Delayed birth in *Protemnodon eugenii*. *Australian Journal of Zoology* **3**, 156–161.
- SHARMAN, G. B. (1963). Delayed implantation in marsupials. In *Delayed Implantation* (ed. A. C. ENDERS), pp. 3–14. Chicago University Press, Chicago.
- SHARMAN, G. B. & PILTON, P. E. (1964). The life history and reproduction of the red kangaroo (*Megaleia rufa*). *Proceedings of the Royal Society of London* **142**, 29–48.
- SHAW, G. & ROSE, R. W. (1979). Delayed gestation in the Potoroo *Potorous tridactylus* (Kerr). *Australian Journal of Zoology* **27**, 901–912.
- SHERMAN, H. B. (1930). Birth of the young of *Myotis austroriparius*. *Journal of Mammalogy* **11**, 495–503.
- SHIELD, J. (1968). Reproduction of the quokka, *Setonix brachyurus*, in captivity. *Journal of Zoology, London* **155**, 427–444.
- SHUMP, K. A. & SHUMP, A. U. (1982a). *Lasiurus borealis*. *Mammalian Species* **183**, 1–6.
- SHUMP, K. A. & SHUMP, A. U. (1982b). *Lasiurus cinereus*. *Mammalian Species* **185**, 1–5.
- SINHA, A. A., CONAWAY, C. H. & KENYON, K. W. (1966). Reproduction in the female sea otter. *Journal of Wildlife Management* **30**, 121–130.
- SINHA, A. A. & ERICKSON, A. W. (1972). Ultrastructure of the placenta of Antarctic seals during the first third of pregnancy. *American Journal of Anatomy* **141**, 317–327.
- SOULSBURY, C. D. (2010). Genetic patterns of paternity and testes size in mammals. *PLoS ONE* **5**, e9581.
- STEWART, B. S. & HUBER, H. R. (1993). *Mivounga angustirostris*. *Mammalian Species* **449**, 1–10.
- STIRLING, I. (1969). Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology* **50**, 573–586.

- STOCKLEY, P. (2002). Sperm competition risk and male genital anatomy: comparative evidence for reduced duration of female sexual receptivity in primates with penile spines. *Evolutionary Ecology* **16**, 123–137.
- STOCKLEY, P. (2003). Female multiple mating behaviour, early reproductive failure and litter size variation in mammals. *Proceedings of the Royal Society of London Series B: Biological Sciences* **270**, 271–278.
- STRELKOV, P. P. (1962). The peculiarities of reproduction in bats (Vespertilionidae) near the northern border of their distribution. In *International Symposium on Methods in Mammalogical Investigation*, pp. 306–311. Brno, Czech Republic.
- STUBBE, M. (1968). Zur Populationsbiologie der Martes—Arten. *Beiträge zur Jagd und Wildforschung* **104**, 195–203.
- TEMTE, J. L. (1985). Photoperiod and delayed implantation in the northern fur seal (*Callorhinus ursinus*). *Journal of Reproduction and Fertility* **73**, 127–131.
- THOM, M. D., JOHNSON, D. D. P. & MACDONALD, D. W. (2004). The evolution and maintenance of delayed implantation in the Mustelidae (Mammalia: Carnivora). *Evolution* **58**, 175–183.
- THOMAS, D. W., FENTON, M. B. & BARCLAY, R. M. R. (1979). Social behavior of the little brown bat, *Myotis lucifugus* I. Mating Behavior. *Behavioral Ecology and Sociobiology* **6**, 129–136.
- THORNHILL, R. (1983). Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *American Naturalist* **122**, 765–788.
- TIDEMAN, C. R. (1993). Reproduction in the bats *Vespadelus vulturnus*, *V. regulus* and *V. darlingtoni* (Microchiroptera, Vespertilionidae) in Coastal South-Eastern Australia. *Australian Journal of Zoology* **41**, 21–35.
- TRAVIS, A. J., JORGEZ, C. J., MERDIUSHEV, T., JONES, B. H., DESS, D. M., DIAZ-CUETO, L., STOREY, B. T., KOPF, G. S. & MOSS, S. B. (2001). Functional relationships between capacitation-dependent cell signaling and compartmentalized metabolic pathways in Murine spermatozoa. *Journal of Biological Chemistry* **276**, 7630–7636.
- TREGENZA, T. & WEDELL, N. (2000). Genetic compatibility, mate choice and patterns of parentage: invited review. *Molecular Ecology* **9**, 1013–1027.
- TYNDALE-BISCOE, C. H. (1968). Reproduction and post-natal development in the marsupial *Bettongia lesueur* (Quoy & Gaimard). *Australian Journal of Zoology* **13**, 577–602.
- TYNDALE-BISCOE, C. H. & RENFREE, M. B. (1987). *Reproductive Physiology of Marsupials*. Cambridge University Press, Cambridge.
- UCHIDA, T. A., INOUE, C. & KIMURA, K. (1984). Effects of elevated temperatures on the embryonic development and corpus luteum activity in the Japanese long-fingered bat, *Miniopterus schreibersii fuliginosus*. *Journal of Reproduction and Fertility* **71**, 439–444.
- UCHIDA, T. A. & MORI, T. (1987). Prolonged storage of spermatozoa in hibernating bats. In *Recent Advances in the Study of Bats* (eds M. B. FENTON, P. RACEY, J. M. V. RAYNOR and J. M. V. RAYNOR), pp. 351–366. Cambridge University Press, Cambridge.
- VAMBUKAR, S. A. (1958). The male genital tract of the Indian Megachiropteran bat *Cynopterus sphinx gangeticus*. *Proceedings of the Zoological Society of London* **130**, 57–77.
- VANPÉ, C., KJELLANDER, P., GAILLARD, J. M., COSSON, J. F., GALAN, M. & HEWISON, A. J. M. (2009). Multiple paternity occurs with low frequency in the territorial roe deer, *Capreolus capreolus*. *Biological Journal of the Linnean Society* **97**, 128–139.
- VAUGHAN, T. A., RYAN, J. M. & CZAPLEWSKI, J. J. (2000). *Mammalogy*. Fourth Edition. Saunders College Publishing, Orlando.
- VERRELL, P. A. (1992). Primate penile morphologies and social systems. *Folia Primatologica* **59**, 114–120.
- VOIGT, C. C., HECKEL, G. & MAYER, F. (2005). Sexual selection favors small and symmetric males in the polygynous greater sac-winged bat *Saccopteryx bilineata* (Emballonuridae, Chiroptera). *Behavioral Ecology and Sociobiology* **57**, 457–464.
- VOLF, J. (1963). Bemerkungen zur Fortpflanzungsbiologie der Eisenbären, *Thalartctos maritimus* (Phipps) in Gefangenschaft. *Zeitschrift für Säugetierkunde* **28**, 163–166.
- VONHOF, M. J., BARBER, D., FENTON, M. B. & STROBECK, C. (2006). A tale of two siblings: multiple paternity in Big Brown bats (*Eptesicus fuscus*) demonstrated using microsatellite markers. *Molecular Ecology* **15**, 241–247.
- VOSS, R. S. (1979). Male accessory glands and the evolution of copulatory plugs in rodents. *Occasional Papers of the Museum of Zoology University of Michigan* **689**, 1–27.
- WAAGE, J. K. (1979). Dual function of the damselfly penis: sperm removal and transfer. *Science* **203**, 916–918.
- WADE-SMITH, J. & RICHMOND, M. E. (1975). Care, management, and biology of captive striped skunks (*Mephitis mephitis*). *Lab Animal Science* **25**, 575–584.
- WADE-SMITH, J. & RICHMOND, M. E. (1978). Reproduction in captive striped skunks (*Mephitis mephitis*). *American Midland Naturalist* **100**, 452–455.
- WADE-SMITH, J., RICHMOND, M. E., MEAD, R. A. & TAYLOR, H. (1980). Hormonal and gestational evidence for delayed implantation in the striped skunk, *Mephitis mephitis*. *General and Comparative Endocrinology* **42**, 509–515.
- WAI-PING, V. & FENTON, M. B. (1988). Nonselective mating in little brown bats (*Myotis lucifugus*). *Journal of Mammalogy* **69**, 641–645.
- WANG, Z., LIANG, B., RACEY, P. A. & WANG, Y. L. (2008). Sperm storage, delayed ovulation, and menstruation of the female Rickett's big-footed bat (*Myotis ricketti*). *Zoological Studies* **47**, 215–221.
- WARD, S. J. (1990). Reproduction in the Western pygmy-possum, *Cercartetus concinnus* (Marsupialia, Burramyidae), with notes on reproduction of some other small possum species. *Australian Journal of Zoology* **38**, 423–438.
- WARD, S. J. & RENFREE, M. B. (1988). Reproduction in males of the feathertail glider *Acrobates pygmaeus* (Marsupialia). *Journal of Zoology* **216**, 241–251.
- WEETMAN, A. P. (1999). The immunology of pregnancy. *Thyroid* **9**, 643–646.
- WEICHERT, C. K. (1940). The experimental shortening of delayed pregnancy in the albino rat. *Anatomical Record* **77**, 31–48.
- WILKINSON, G. S. & MCCracken, G. F. (2003). Bats and balls: sexual selection and sperm competition in the chiroptera. In *Bat Ecology* (eds T. H. KUNZ and M. B. FENTON), pp. 128–155. University of Chicago Press, Chicago.
- WILLET, E. L. & OHMS, J. I. (1957). Measurement of testicular size and its relation to production of spermatozoa by bulls. *Journal of Dairy Science* **40**, 1559–1569.
- WILSON, D. E. & REEDER, D. M. (2005). *Mammal Species of the World: A Taxonomic and Geographic Reference*. 3rd Edition. Johns Hopkins University Press, Baltimore.
- WIMSATT, W. A. (1942). Survival of spermatozoa in the female reproductive tract of the bat. *Anatomical Record* **83**, 299–307.
- WIMSATT, W. A. (1944). An analysis of implantation in the bat *Myotis lucifugus lucifugus*. *American Journal of Anatomy* **74**, 355–411.
- WIMSATT, W. A. (1945). Notes on breeding behavior, pregnancy, and parturition in some Vespertilionid bats of the Eastern United States. *Journal of Mammalogy* **26**, 23–33.
- WIMSATT, W. A. (1963). Delayed implantation in the Ursidae with particular reference to the black bear (*Ursus americanus* Pallas). In *Delayed Implantation* (ed. A. C. ENDERS), pp. 49–76. University of Chicago Press, Chicago.
- WIMSATT, W. A. (1979). Reproductive asymmetry and unilateral pregnancy in Chiroptera. *Journal of Reproduction and Fertility* **56**, 345–357.
- WIMSATT, W. A., KRUTZSCH, P. H. & NAPOLITANO, L. (1966). Studies on sperm survival mechanisms in the female reproductive tract of hibernating bats. I. Cytology and ultrastructure of intra-uterine spermatozoa in *Myotis lucifugus*. *American Journal of Anatomy* **119**, 25–59.
- WINDSOR, D. P. (1997). Mitochondrial function and ram sperm fertility. *Reproduction, Fertility and Development* **9**, 279–284.
- WRIGHT, P. L. (1942). Delayed implantation in the long-tailed weasel (*Mustela frenata*), the short-tailed weasel (*Mustela cicognani*), and the marten (*Martes americana*). *Anatomical Record* **83**, 341–353.
- WRIGHT, P. L. (1963). Variations in reproductive cycles in North American mustelids. In *Delayed Implantation* (ed. A. C. ENDERS), pp. 77–97. University of Chicago Press, Chicago.
- WRIGHT, P. L. (1966). Observations on the reproductive cycle of the American badger (*Taxidea taxus*). In *Comparative Biology of Reproduction in Mammals* (ed. I. W. ROWLANDS), pp. 27–45. Academic Press, New York.
- WRIGHT, P. L. & COULTER, M. W. (1967). Reproduction and growth in Maine fishers. *Journal of Wildlife Management* **31**, 70–87.
- WRIGHT, P. L. & RAUSCH, R. A. (1955). Reproduction in the wolverine, *Gulo gulo*. *Journal of Mammalogy* **36**, 346–355.
- YAMAGUCHI, N., SARNO, R. J., HONSON, W. E., O'BRIEN, S. J. & MACDONALD, D. W. (2004). Multiple paternity and reproductive tactics of free-ranging American minks, *Mustela vison*. *Journal of Mammalogy* **85**, 432–439.
- ZARROW, M. X. & CLARK, J. H. (1968). Ovulation following vaginal stimulation in a spontaneous ovulator and its implications. *Journal of Endocrinology* **40**, 343–352.
- ZEH, J. A. & ZEH, D. W. (1996). The evolution of polyandry I: Intra-genomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London Series B: Biological Sciences* **263**, 1711–1717.
- ZEH, J. A. & ZEH, D. W. (1997). The evolution of polyandry II: post-copulatory defenses against genetic incompatibility. *Proceedings of the Royal Society of London Series B: Biological Sciences* **264**, 60–75.
- ZEH, D. W. & ZEH, J. A. (2000). Reproductive mode and speciation: the viviparity-driven conflict hypothesis. *BioEssays* **22**, 938–946.
- ZIEGLER, L. (1843). *Beobachtungen über die Brunst und den Embryo der Rehe*. Helwingsche Hofbuchhandlung, Hannover.

(Received 11 January 2013; revised 12 January 2014; accepted 16 January 2014)