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Original investigation

Photoperiod and the timing of reproduction in *Antechinus flavipes* (Dasyuridae: Marsupialia)

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Abstract

The effect of an artificial, unchanging photoperiod regime was examined in comparison to a natural photoperiodic regime on the reproductive pattern in *Antechinus flavipes*, a small dasyurid marsupial which in the wild has a short, highly synchronized mating period. Females held under a photoperiod of LD 12:12 showed delayed sexual maturity and only one individual entered oestrus, about 3 weeks after females under natural photoperiod. Oestrus could be induced in the remaining females by increasing the photoperiod by 1 min/day for at least 3–4 weeks. In contrast to the females, males under artificial and natural photoperiod showed a similar pattern of maturity and decline of reproductive condition and senility. Only some aspects of sexual maturity were delayed and others were unsynchronized in males under LD 12:12 regime compared to the males held under the natural photoperiod. Our study suggests that, especially in females, changing photoperiod is important in synchronizing reproductive events in *A. flavipes*.

Key words: *Antechinus flavipes*, marsupial, photoperiod, reproduction

Introduction

Photoperiod and endogenous circannual rhythms are important in regulating reproductive cycles in many placental mammals (Bronson 1985; Goldman 2001). Circannual rhythms can be pronounced, with some species demonstrating repeated and approximately yearly reproductive cycling while held under seasonally constant conditions of photoperiod and temperature (e.g., ground squirrels and sheep, Bronson 1985; Körtner and Geiser 2000; Goldman 2001). However, many other mammals exhibit non-circannual seasonality. These species, when held under seasonally constant conditions of photoperiod and temperature, remain in the reproductive state proscribed by the proximate photoperiodic cue, and change reproductive status only in response to a change in the photoperiod (Bronson 1985; Goldman 2001). Whereas placental mammals have received considerable attention with respect to interactions between photoperiod and reproduction, few studies have been performed to determine whether similar control mechanisms exist for marsupials, especially for the order Dasyuromorphia (McAllan 2003).

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Reproduction in the marsupial genus *Antechinus* (Dasyuromorphia) is typified by a short, highly synchronized mating period, the timing of which varies only little from year to year (Dickman 1982; Lee et al. 1982; McAllan et al. 2006). Females are monoestrous and all males die shortly after mating (Woolley 1966; Wood 1970). While the pattern of the reproductive behaviour has been extensively monitored, little work has been done to establish the mechanisms by which reproduction is controlled (Dickman 1985; Scott 1986; Woolley 1966; Wood 1970; McAllan et al. 1991). Most work has focused on members of the *A. stuartii*/*A. agilis* complex with few studies exploring mechanisms of regulation of the reproductive cycle in other species (Dickman 1985; Scott 1986; Woolley 1966; Wood 1970; McAllan et al. 1991).

Dickman (1985), on the basis of experimental evidence, has suggested that photoperiod may cue an endogenous rhythm in three species of *Antechinus*. In this study *A. stuartii*, *A. flavipes*, and *A. swainsonii* were placed under LD 12:12 photoperiod at differing times from late-April to June (when the natural photoperiod is decreasing towards the winter solstice, in late June), which resulted in unsynchronized reproductive activity when compared to animals held under the naturally changing cycle, although experimental animals did reproduce at an approximately similar time of year to those held under the natural photoperiod. Dickman (1985) found that the laboratory conditions of his study also affected reproductive synchrony under both naturally changing and LD 12:12 photoperiod, indicating an effect of social organization. McAllan and Dickman (1986) and McAllan et al. (1991) demonstrated that a discretely increasing photoperiod (rate of change of photoperiod) may synchronize reproduction in *A. stuartii*. Recently McAllan et al. (2006) developed this paradigm further by demonstrating a correlation between the changing photoperiod and timing of reproduction for all species of *Antechinus*, and that most wild populations of *A. flavipes* may be cuing to an increasing rate of change of photoperiod of approximately 77–97 s per day. Thus, the present study was designed to provide experimental evidence regarding the extent of the photoperiodic control of reproduction in the yellow-footed antechinus, *A. flavipes*.

Material and methods

Experimental conditions

Experimental animals consisted of 17 laboratory reared *A. flavipes,* the offspring of pregnant females wild caught in the Adelaide area, South Australia (34°50′S, 138°30′ E), and all experiments were conducted in Adelaide. They were fed a mixture of moistened dog or puppy chow and tinned cat food which was exchanged daily late in the afternoon. Dry cat chow and water were available ad libitum. All animals were housed under a natural photoperiod of Adelaide while with their mothers or other juveniles until the beginning of the experiment, when all juveniles were weaned and were separated from other individuals. From 23 February all animals were housed individually in cages ($45 \times 30 \times 16$ cm) provided with hard wood shavings and nesting boxes containing nesting material. Four males and five females were maintained under natural photoperiod conditions of Adelaide throughout the experimental period. Four male and four females were placed under an unchanging artificial photoperiod of LD 12:12. This photoperiod was chosen as it is the longest photoperiod prevailing at the reported mating times in *A. flavipes* (Schmidt and Mason 1973). Females under artificial photoperiod which had not shown signs of oestrus by late September (8 weeks after those under natural photoperiod exhibited oestrus) were exposed to an increase in photoperiod by 1 min/day starting from the original cycle of LD 12:12. This approximates the change in photoperiod naturally experienced by *A. flavipes* during the mating season (McAllan et al. 2006).

Females

Females were checked once every 1–2 weeks and during the mating season every 2–3 days, for the presence of epithelial cells, which indicate the onset of oestrus (Selwood 1982; McAllan et al. 1991). Urine samples were taken when possible. When females did not urinate a urogenital sinus smear was taken by carefully wiping the urogenital sinus over a clean slide. Samples were examined for the presence of epithelial cells and scored on a scale similar to that of Selwood (1982) and McAllan et al. (1991). When individuals gave

birth, urogenital sinus smears were discontinued. The pouch change associated with sexual maturity, oestrus, and pregnancy or pseudo-pregnancy is an easily observable phenomenon in *Antechinus* (Woolley 1966; Dickman 1985; McAllan et al. 1991) and the pouch changes associated with the reproductive sequence were scored following McAllan et al. (1991). The urogenital sinus of *A. flavipes* becomes very swollen and flushed during oestrus and this indicator was also included in the scoring system (see McAllan et al. 1991).

Males

Males were checked once every 1–2 weeks. The scrotal width was measured with vernier calipers. The condition of the pelage, the pigmentation of the testes and the maturation of the penis were monitored essentially as described by Woolley (1966) and McAllan et al. (1991). The presence of sperm in the urine (spermatorrhoea), which is an indicator of sexual maturity in male dasyurids (Woolley 2003) was also recorded as was the change of the size of the urethral bulbs or Cowper's glands, which are paired sets of glands that lie on either side of the urogenital sinus; according to Rodger and Hughes (1973) these lie adjacent to the crura of the penis. They enlarge just prior to the mating period in *A. stuartii* and *A. flavipes* and in *A. stuartii* increase in response to presence of testosterone (Woolley 1966; McAllan et al. 1991; McAllan 1998). In *A. flavipes*, they were monitored throughout the year by manipulating the urogenital sinus region and assessing their degree of enlargement on a six-point scale (McAllan et al. 1991). Measurements were discontinued in October because of the decline in male numbers, because of the naturally occurring male mortality that occurs after the breeding season (Woolley 1966).

Mating

When females were observed to be in oestrus they were placed into a large cage ($60 \times 40 \times 27$ cm). A male was then introduced into the cage and animals were observed to ensure that there was no agonistic behaviour. Animals were separated when sperm was apparent in the females' urine or after mating was observed. Subsequent pairings were set up when animals appeared to be incompatible (McAllan et al. 1991).

Wild population versus controls

To assess whether captivity affected reproductive activity in *A. flavipes*, a wild population was live-trapped and released using Elliot box traps during the breeding season at two sites in South Australia (34°32′ S, 138°30′E; and 35°S 23′E). Females were assessed for reproductive condition, mating activity, and subsequent births, and males were assessed for reproductive maturity and signs of reproductive senility, as described above.

Statistical analysis

Reproductive data were analysed by repeated measures Analysis of Variance, using treatment, and date of measurement as variables for the duration of the experiment. All male reproductive variables were compared on the same day for each group in each experiment throughout the monitoring period. In females, the peak of the brief presence of epithelial cells indicating reproductive receptivity, may be evident between weekly measurements of reproductive parameters. Therefore, female data for presence of epithelial cells were compared on the day of measurement for the mating period, at all other times data were compared at the once weekly measurement.

Data were also analysed by the time of the year that the reproductive event occurred for each individual by numbering the days throughout the year, determining the week number when the event occurred, and then performing an unpaired *t*-test on the day numbers for each treatment group. In males, this was for the date when variables reached their maximum (scrotal width, maximal size of bulbourethral glands), or for the date of first appearance of secondary sex characteristics (spermatorrhoea, palpation of bulbourethral glands, fur loss, and other signs of male deterioration). In females, this was for the maximum numbers of epithelial cells, birth, and maximum pouch change. A Mann–Whitney *U*-test was performed on data when the assumption of equal variances for *t*-tests was not met.

Results

Females

Distinct differences in the timing of reproduction were observed between animals in natural and artificial photoperiod. Sexual maturity, evident from the eversion of the nipples, and changes to the pouch and urogenital sinus (see Selwood 1982; Dickman 1985; McAllan et al. 1991) were completed in the females under natural photoperiod by the last week of June. In contrast, in females

under artificial photoperiod this was not observed until late July, significantly later than the control females ($P<0.01$, Fig. 1a). All females under natural photoperiod came into oestrus and mated between 17 and 27 July (days 198–208) and gave birth between 14 and 25 August (days 226–237, Figs. 1a, b). In contrast, only one female under LD 12:12 came into oestrus and mated during 10–14 August and gave birth on 8 September (day 251). The onset of oestrus activity in the remainder of females under artificial photoperiod did not occur until late October, after the photoperiod had been increased by 1 min/day for nearly 4 weeks, significantly later than the control females ($P<0.05$, Mann-Whitney U-test, Figs. 1a, b). Matings in these individuals were observed between 23 October and 25 November (Figs. 1a, b). These females underwent the characteristic pouch changes associated with pregnancy, but did not give birth, presumable due to the lack of sperm in the surviving males (i.e. pseudo-pregnancy, see Woolley 1966). Maximum pouch changes associated that occur just prior to birth (or at the end of pseudo-pregnancy) occurred significantly later in females under artificial photoperiods ($P<0.05$, Mann–Whitney U test, Figs. 1a, b).

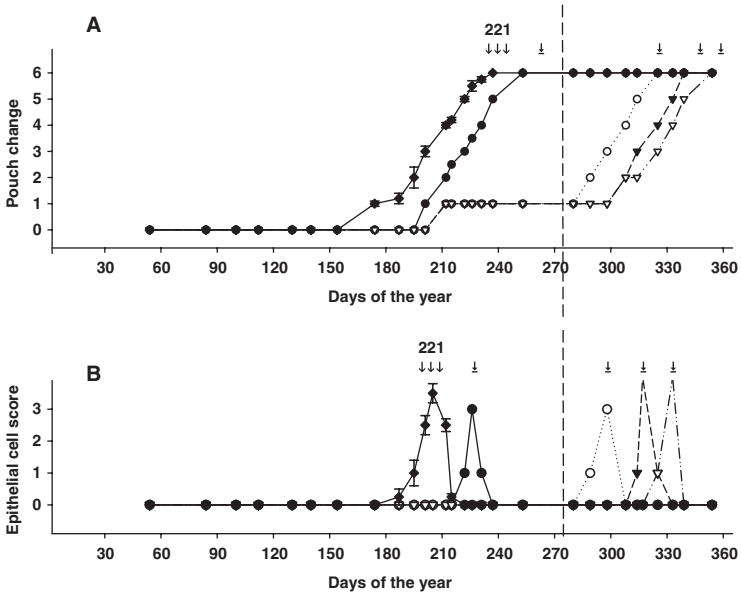

Fig. 1. (A) Pouch change in females from February to December (days 54–364). Females held under natural photoperiod are represented by solid line and solid diamonds, with each point representing the mean values (± standard errors) at that time for this group. Solid arrows with numbers of individuals above indicate the time that the control females gave birth. Individual females held under LD 12:12 photoperiod are indicated by different separate symbols (solid circles, solid line; open circles dotted line; solid triangle dashed line; open triangle dotted and dashed lines). Underlined arrows indicate parturition or times when maximum pouch size was observed for these individual LD 12:12 females. The vertical dashed line indicates the time when photoperiod was increased by 1 min per day. (B) Presence and change in epithelial cells in the urine of females from February to December (days 54–364). Females held under natural photoperiod are represented by solid line and solid diamonds, with each point representing the mean values at that time for this group, and bars are standard errors. Solid arrows with number above indicate the time that the control females mated. Individual females held under LD 12:12 photoperiod are indicated by different separate symbols (solid circles, solid line; open circles dotted line; solid triangle dashed line; open triangle dotted and dashed lines). Underlined arrows indicate mating times for these individual LD 12:12 females. The vertical dashed line indicates the time when photoperiod was increased by 1 min per day.

Males

The two experimental groups of males also exhibited some significant differences in reproductive synchrony between groups, although these were not as distinct as between female groups. The scrotal width increased until May/June in both groups and declined thereafter. Only in August and September were significant differences ($P<0.05$) observed in scrotal widths between the two groups (Fig. 2a). Spermatorrhoea first occurred in males under natural photoperiod in late May and the presence of sperm and the following decline corresponded to the testes examined histologically by Inns (1976). In contrast, males under LD 12:12 had no sperm in the urine until late June, significantly later than control males ($P<0.05$, *t*-test, Figs. 2a, 3a, b). Sperm had disappeared from the urine in males under natural photoperiod by mid-August, but were still observed in the urine of males under artificial photoperiod until early to mid-September (Figs. 3a, b).

The first observation of the immature penis occurred almost 1 month earlier in males held under the natural photoperiod than under the artificial photoperiod ($P<0.05$, Mann–Whitney *U*-test, Fig. 3c). However, consequent maturation occurred at a similar rate for both groups of males (Fig. 3c, d). The change in pigmentation and reduction in fur coverage of the scrotum began a few weeks earlier in

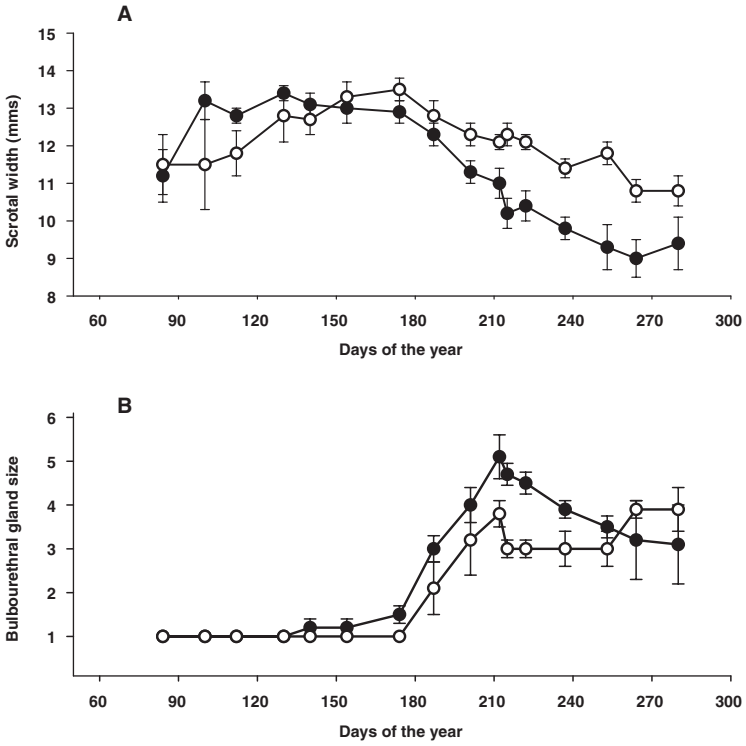

Fig. 2. (A) Scrotal width in millimeters of males from March to October (days 84–280). Solid circles joined by solid lines are data for males under the natural photoperiod, and open circles joined by solid lines are data for males under L:D 12:12 photoperiod. Data are means ± standard errors, and asterisks indicate where data points were significantly different between groups. (B) Bulburethral gland size in males from March to October (days 84–280). Solid circles joined by solid lines are data for males under the natural photoperiod, and open circles joined by solid lines are data for males under LD 12:12 photoperiod. Data are means ± standard errors, and asterisks indicate where data points were significantly different between groups.

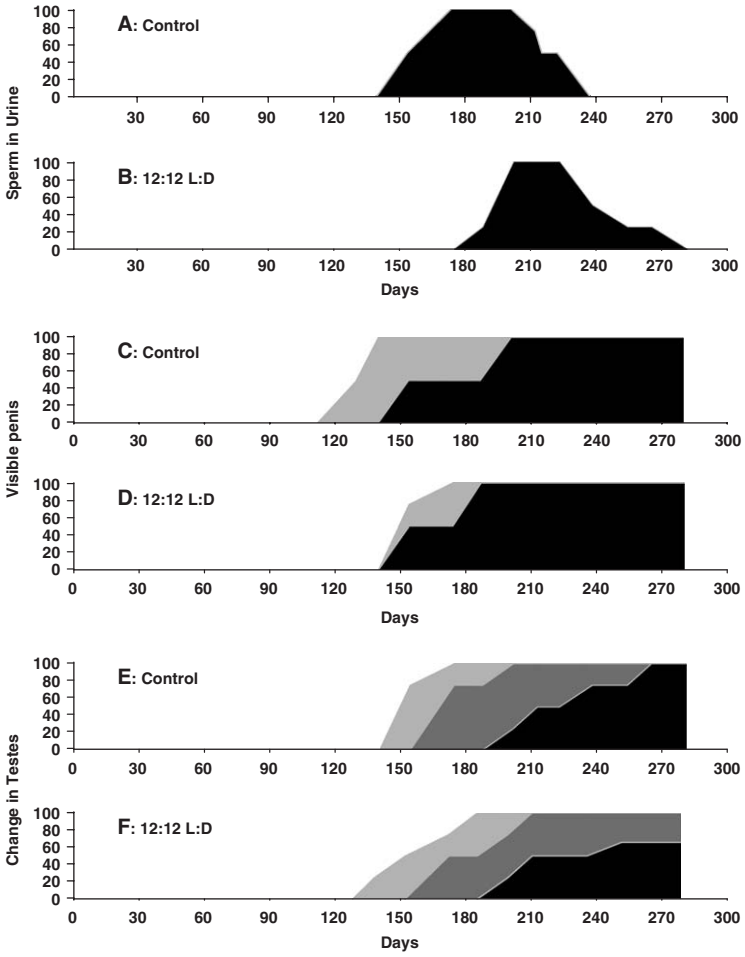

Fig. 3. External indicators of reproductive change in males from March to October (days 84–280). (A) and (B) Percentage of males exhibiting spermatorrhoea in (A) control (natural photoperiod) and (B) experimental (L:D 12:12 photoperiod) groups. (C) and (D) Percentage of males exhibiting signs of sexual maturity, in this instance an immature penis (light grey shading) and a mature penis (black shading), in (C) control (natural photoperiod) and (D) experimental (L:D 12:12 photoperiod) groups. (E) and (F) Percentage of males exhibiting external signs of decline, in (E) control (natural photoperiod) and (F) experimental (L:D 12:12 photoperiod) groups. The signs of decline are discerned by the change in the external appearance of the pendulous testes in their scrotal sac. Descriptors are dark-pigmented skin, retractile to body (light grey shading), dark pigmented skin, fur loss, and no longer able to retract scrotal sac to body (dark grey shading), and dark pigmented wrinkled skin, complete fur loss, and no longer able to retract scrotal sac to body (black shading).

males under artificial photoperiod and the following decline in condition appeared more erratic than in males held under the natural photoperiod, although any apparent differences were not significant between groups (Figs. 3e, f). The increase in size of the urethral bulbs occurred earlier in males under the natural photoperiod regime, beginning in late May, but was not observed until early June in males under LD 12:12 ($P<0.05$, Fig. 2b). However, the consequent increase in urethral bulb dimensions was similar across

the year in both groups except for two measurements in early August ($P<0.05$, Fig. 2b).

Wild population versus controls

The wild female population exhibited oestrus activity in mid-late July (days 199–208), and parturition occurred in mid-late August (days 230–239). Males declined rapidly after the mating period, and no males were trapped by the time the wild females had given birth in late August (i.e. suggesting complete male post-mating mortality).

Discussion

The results of the present study provide strong experimental evidence that changing photoperiod is involved in the precise control of reproduction in *A. flavipes*. This was especially apparent in females, whereas in males the reliance on photoperiodic change to time reproductive events was less pronounced.

The importance of photoperiod in the timing of reproduction is demonstrated by the lack of oestrous in all but one female held under LD 12:12 photoperiod at a time when mating normally occurs in this species, and also by the induction of oestrus activity in the remaining experimental females by an increase in photoperiod of approximately 1 min per day, similar to that experienced by animals when under the natural cycle. However, in contrast to females under the natural photoperiod, which experience 10.5 h of light per day during the reproductive period, the absolute photoperiod experienced by experimental females was 12 h of light per day. The changing photoperiod induced oestrous even though the absolute photoperiod was longer than that experienced by any wild population in South Australia during the mating period (see McAllan et al. 2006 for discussion). This evidence and the different prevailing absolute photoperiods observed during the mating period for *A. flavipes* populations at different latitudes (McAllan et al. 2006) suggest that the length of photoperiod itself is not used as a cue for reproduction, but that the change of photoperiod is the proximal cue.

All females in the present study, in both wild and captive populations, exhibited oestrus cycling within a 12 day period when the natural photoperiod was increasing 70–82 s per day. This rate of increase does not occur at any other time of year, whereas the absolute photoperiod experienced during mating activity will occur twice a year, once before and once after the winter solstice. Animals did respond to the change in photoperiod, but less synchronized, perhaps because of the fact that increasing photoperiod by 60 s per day did not precisely mimic the rate of change of photoperiod experienced by females under natural light.

While photoperiodic change is an important proximate cue, control of reproduction in *A. flavipes* also appears to have an endogenous component. One female demonstrated reproductive activity under LD 12:12 photoperiod, although not in synchrony with the females held under naturally changing photoperiod. Moreover, males under LD 12:12 underwent reproductive maturity and subsequent senility at approximately the same time as the males experiencing the natural photoperiod, although in a less synchronized manner. An endogenous component to reproduction has also been described for *A. stuartii* (Dickman 1985; Scott 1986) and also proved experimentally for *A. stuartii* (McAllan et al. 1991). The males under the experimental photoperiod in the present study demonstrated delayed spermatorrhea and external characteristics (e.g., external presence of the penis in the urogenital sinus) when compared to males experiencing natural photoperiod. However, the initial and final deteriorating stages of testes change occurred earlier in males under experimental photoperiod than those under natural photoperiod. While males in the wild population disappeared before the young were born, the male "die-off" was less pronounced in males under natural photoperiod in captivity. This has been observed in many studies (Selwood 1982; Dickman 1985; Scott 1986; McAllan et al. 1991) and is believed to be because of social factors in the wild (most laboratory-based studies hold males separately, including the present study) and because excess

food is readily available to captive males (Selwood 1982; Dickman 1985; Scott 1986; McAllan et al. 1991). In males held under LD 12:12 some aspects of maturity and senility were delayed and others were precocious. This suggests that an endogenous mechanism underlies the biology of males, however, changing photoperiod may help to synchronize the endogenous mechanism. This has been demonstrated for other dasyurid marsupials (see McAllan 2003) and also for *A. stuartii* (McAllan et al. 1991).

In females, the strength of an endogenous rhythm can be seen in the initial change of the pouch, eversion of the nipples and thinning of the pouch hair, all of which are significantly but not synchronously delayed in females held under the experimental photoperiod. When coupled with the observation of one female entering oestrus under the constant photoperiod, these observations suggest that the reproductive cycle is not exclusively controlled by photoperiod. Similar results were found for *A. stuartii* (McAllan et al. 1991), although in that experiment, this was shown when the complete changing photoperiodic cycle was shifted by 2 months, beginning at different times of the seasonal cycle.

Other experiments determining the effect of unchanging photoperiods on *A. stuartii/agilis* demonstrated that long photoperiods (LD 14:10) suppressed ovulation, and short photoperiods (LD 10:14) induce asynchronous ovulations (Scott 1986). In this study, animals were exposed to these photoperiods approximately 1 month before the winter solstice, after which photoperiod begins to increase (Scott 1986), considerably later than the present study, where animals were placed under experimental conditions 3 months before the winter solstice. The only other experiment using unchanging photoperiod with the genus *Antechinus* exposed to LD 12:12 beginning at differing times from late-April to June in *A. stuartii, A. flavipes* and *A. swainsonii* (Dickman 1985), and these females displayed oestrus in an unsynchronized manner, but at a similar time to females under the natural photoperiod. In the present experiment, animals were placed under the unchanging photoperiod at least 2 months earlier than previous studies, demonstrating that changing photoperiod is necessary to synchronize reproductive events, and that without prolonged exposure to changing photoperiods "breakthrough" reproduction using the endogenous cues (Goldman 2001) is less likely to occur.

While "true" endogenous rhythms are usually shown experimentally by following the cycle in individuals for at least a second year (Goldman 2001; Körtner and Geiser 2000), this is not possible in a mammal such as *A. flavipes* with a male life expectancy of only 11.5 months, and where few females live for longer than 18 months (Woolley 1966; Inns 1976; Smith 1984). It also appears that *A. flavipes* and *A. stuartii/agilis* are unusual in their endogenous and photoperiodic responsiveness for cuing for reproduction because many photoperiodically sensitive short-lived mammals do not use circannual rhythmicity to help cue reproduction under constant conditions (Goldman 2001).

The coupling of endogenous and photoperiodic responsiveness is further demonstrated by the use of only 1 min increase per day to induce reproductive activity. However, other mammals are also known to be able to use 1 min pulses to entrain circadian activities (Steinlechner et al. 2002), and are also known to use dim light to enhance other cues (Gorman et al. 2005). Thus, the use of precise or sensitive components of the photoperiod to proximally cue for the best time of year to reproduce, i.e. the ultimate factor for use of these proximate cues, is not particularly unusual, although the use of a precise increasing daylength to cue for mating activity is known only from the *Antechinus* genus at present, and our study has extended the knowledge of photoperiodism and control of reproduction in this marsupial genus.

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Zusammenfassung

Photoperiode als Zeitgeber für Reproduktion bei *Antechinus flavipes* (Dasyuridae: Marsupialia)

Der Einfluss einer künstlichen, konstanten Photoperiode auf die Reproduktion bei *Antechinus flavipes*, einem kleinen Beuteltier, das im Freiland eine kurze, genau synchronisierte Paarungszeit hat, wurde im Vergleich zu einer natürlichen Photoperiode untersucht. Weibchen unter einer LD 12:12 Photoperiode zeigten verspätete sexuelle Reife, und nur ein Tier begann Oestrus, etwa drei Wochen nach den Weibchen unter natürlicher Photoperiode. Oestrus konnte bei den restlichen Weibchen durch eine Verlängerung der Photoperiode um 1 Min/Tag für mindestens 3–4 Wochen induziert werden. Im Gegensatz zu den Weibchen zeigten Männchen einen ähnlichen Verlauf von Reife, Schwinden von Reproduktivität und Senilität. Nur einige Aspekte der sexuellen Reife in Männchen unter LD 12:12 waren verspätet und andere nicht synchronisiert im Vergleich zu Männchen unter natürlicher Photoperiode. Unsere Untersuchung deutet an, dass eine wechselnde Photoperiode bei der Synchronisation von reproduktiven Vorgängen speziell bei Weibchen von *A. flavipes* wichtig ist.

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