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Reproductive patterns in chromosomally distinct races of *Phyllodactylus marmoratus* (Lacertilia: Gekkonidae) in south-western Australia

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Abstract

An examination of 677 museum specimens of three chromosomal races of *Phyllodactylus marmoratus* in south-western Australia showed different reproductive patterns in the two adjacent and abundant races, 2n=34 and 2n=36. Data for the 2n=32 race are very limited.

Females of all races were gravid in spring, but yolky follicles may occur in all seasons except mid-summer; the 2n=34 race also had gravid females in winter. Females with both eggs and yolky follicles were recorded in 2n=34 and 2n=36 races; over 30% of females had single egg clutches. Males of the 2n=36 race had largest testicular volumes in summer-autumn, a pattern similar to previous studies; males of the 2n=34 race had maximum testicular volumes in spring.

Introduction

The gekkonine gecko *Phyllodactylus marmoratus* has a wide distribution across southern Australia, a distribution that includes four discrete chromosomal races (King and Rofe 1976, King and King 1977).

In south-western Australia three races, 2n=36, 2n=34 and 2n=32, occur along the southern and western coasts in the dominant winter rainfall areas. The 2n=32 race is confined to a small area around Broke Inlet, central to the distribution of the 2n=34 race that occurs from the Abrolhos Is in the north around to Cape Arid in the east. The 2n=36 race extends from east of Cape Arid along the coast and into South Australia (King and King 1977).

An examination of reproduction in *P. marmoratus* was undertaken by King (1977) in South Australia, a region representing the 2n=36 and 2n=36 ZZ/ZW chromosome races (King and Rofe 1976). This histological assessment of the male and female reproductive cycles showed a reproductive strategy based on delayed fertilisation with females employing oviducal sperm storage over winter. A detailed analysis of meiosis in males revealed that chiasmata frequency was seasonally

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cyclic for both interstitial and terminal chiasmata. Sperm used for insemination and fertilisation had the lowest total chiasma frequency but greatest range in interstitial chiasma frequency. This suggests that sperm with the greatest range in genetic variation are used for fertilisation (King and Hayman 1978).

A recent examination of the three chromosomal races of *P. marmoratus* in south-western Australia has resulted in the description of the 2n=36 race as a separate subspecies *P. m. alexanderi* (Storr 1987).

It has been the purpose of this study to examine the broad reproductive patterns of the three chromosomal races in the south-west and compare them with the data presented from South Australia (King 1977).

Materials and methods

This study is based on the examination of 677 specimens of *Phyllodactylus marmoratus* from south-western Australia. Specimens have been collected opportunistically over a 50 year period and represent 155 individuals of the 2n=36 race, 477 of the 2n=34 race and 45 of the 2n=32 race. The 2n=34 and 2n=36 races were distinguished by the criteria of Storr (1987). The 2n=32 individuals were those collected from the Mt Chudalup-Walpole area.

Snout-vent length (SVL) was measured on all specimens. Mid-ventral and lateral incisions were then made to examine reproductive tracts. Maximum length and width of testes, ovarian follicles, and oviducal eggs were measured by one of us (SJG) using dial vernier calipers to the nearest 0.1 mm.

Females were judged as adult by the presence of thickened or convoluted oviducts and/or the presence of enlarged yolked follicles or eggs; reproductively active females were those with yolky follicles, eggs or both. Females with oviducts previously removed were excluded from analysis. Males showed considerable variation in testicular size but were deemed adult by expanded efferent ducts and enlarged testes. Reproductive information was assessed by month regardless of year of collection.

The volume of testes, follicles or eggs was estimated to the nearest 0.1 mm using the equation for a prolate spheroid $V = 4/3\ (1/2)\ (w/2)^2$ where 1 is length and w is width.

Data are summarised as mean ± standard deviation and sample size. Significance differences were determined from t-tests comparing means.

Results

Comparisons of male and female monthly reproductive activity were made for island and mainland groups and south coast and west coast groups of the 2n=34 race. No significant differences were detected in number of reproductively active individuals for those months where $n \geqslant 5$, consequently data are combined for this race. Females on south coast islands were gravid in winter, but there was no comparative mainland data over the same period.

Females

The period of reproductive activity of different chromosome races is presented (Figure 1). Eggs or developing yolky follicles were present in all months for the 2n=34 race except February and March. Samples of the 2n=36 race, *P. m. alexanderi,* were less representative of the year, but also suggest lower reproductive activity over the late summer-autumn period. Data for the 2n=32 were inadequate to determine the extent of the period of reproductive activity.

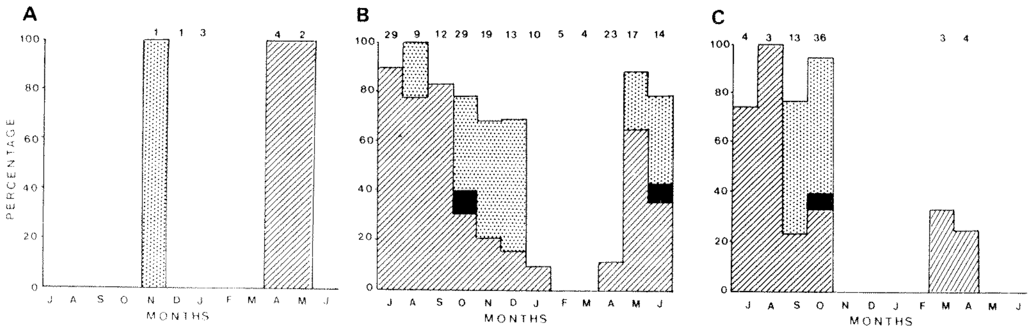

Figure 1 Percentage of reproductively active *Phyllodactylus marmoratus* females, proportioned according to presence of yolky follicles (cross hatching), eggs (stippling) or both (blocked) on a monthly basis. Number of adult females examined for each month is given for [A] 2n=32, [B] 2n=34 and [C] 2n=36.

Table 1 Size of reproductively active females and mean clutch volume in the three chromosomal races of *Phyllodactylus marmoratus* in south-western Australia.

Race	SVL of Smallest Reproductive ♀ (mm)	Mean SVL of Gravid ♀♀ (mm)	Mean Clutch Volumes (mm^3) 1 egg	2 eggs	Maximum Clutch Volume (mm^3)
32	49.3	55.0 (1)		474.4 (1)	474.4
34	39.4	48.1 ± 4.1 (43)	285.9 ± 106.1 (20)	597.7 ± 198.6 (23)	1015.4
36	37.5	447.5 ± 3.5 (29)	203.1 ± 88.7 (9)	469.5 ± 208.2 (20)	1017.2

Single egg clutches were recorded in 20 of the 43 (46.5%) gravid 2n=34 females and 9 of the 29 (31%) gravid 2n=36 females; the only gravid 2n=32 had a two egg clutch (Table 1). Females with both oviducal eggs and yolked ovarian follicles were recorded in the 2n=34 race during October and June and in the 2n=36 race during October (Figure 1). Single yolky follicles were recorded in 21 of the 83 (25.3%)

females with developing follicles in the 2n=34 race, 2 of the 25 (8%) females in the 2n=36 race and 1 of the 6 (16.7%) females in the 2n=32 race. Three 2n=34 females had 3 yolked follicles of similar size.

Mean clutch volumes in the 2n=34 (Table 1) were larger than those in 2n=36 for both single and double egged clutches; this difference was significant ($p<0.05$) for double egg clutches. However, the maximum calculated volumes in both races were almost identical (Table 1). There was no difference in SVL of females with single or double egg clutches for either the 2n=34 [48.0 ± 3.2(20) v. 49.1 ± 3.2(23)] or 2n=36 [48.2 ± 2.3(9) v. 47.1 ± 3.9(20)] races. Females with longer SVLs had larger clutches in the double egged ($r=0.511$, $n=23$, $p<0.01$), but not single egged groups of the 2n=34 race; no significant correlations existed in the 2n=36.

Males

Testicular volumes for the three chromosomal races are presented in Figure 2.

The general pattern of the 2n=34 race was for highest volumes during spring and a decrease over summer. The highest volumes in the 2n=36 race occurred in summer and autumn; data for 2n=32 are inconclusive. In September ($p<0.05$) and

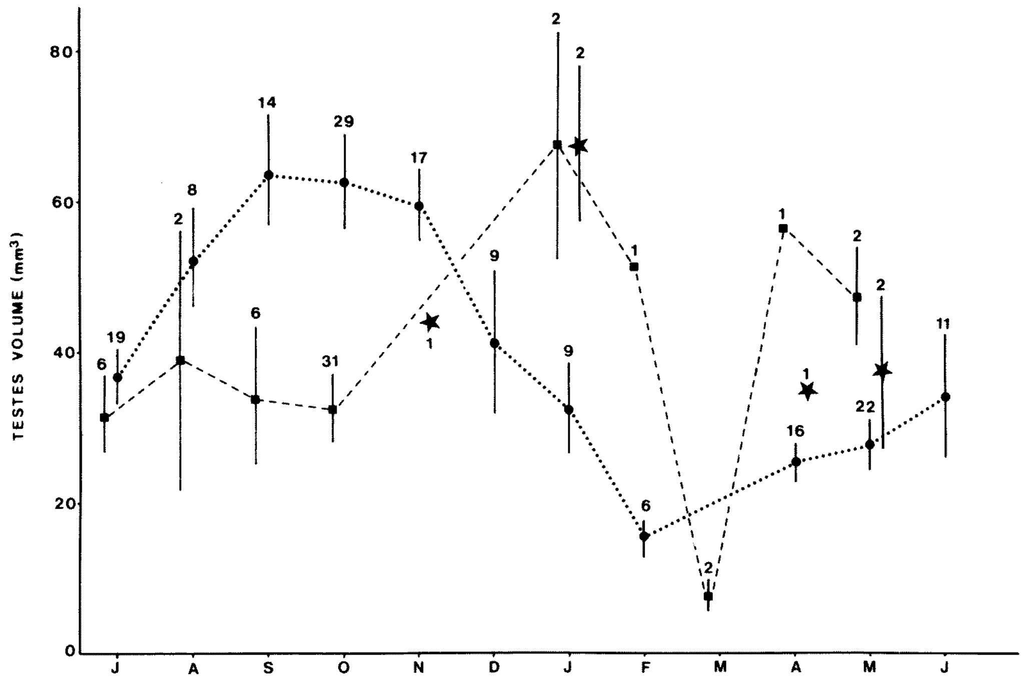

Figure 2 Monthly variation in testes volume (mm^3) of *Phyllodactylus marmoratus* from 2n=32 (stars), 2n=34 (circles) and 2n=36 (squares). Data are presented as means ± SE (n).

October ($p<0.01$) the 2n=34 race had larger volumes, while in May ($p<0.05$) the 2n=36 race had the greater volume; all other comparisons between species did not differ significantly.

Discussion

In a detailed histological examination of reproduction, King (1977) determined that *P. marmoratus* had oviducal sperm storage and delayed fertilisation. The examination of testes weight and meiotic activity suggested maximum spermiogenesis and insemination in late summer and autumn with fertilisation occurring in spring and early summer from the stored sperm (King 1977).

Our examination of the broad reproductive pattern in the 2n=36 subspecies, *P. m. alexanderi,* is in close agreement with King's earlier findings for this and that of the 2n=36 ZZ/ZW races. Males have maximum testicular volume in summer and autumn (Figure 2) whereas oviducal eggs occur in females in the spring (Figure 1). Our data are insufficient, however, to record the extent or intensity of the entire cycle as samples are not available from throughout the year.

Paired oviducal eggs that were laid simultaneously were recorded by King (1977) for *P. m. alexanderi* in South Australia. In the Western Australian data, 31% of gravid females had single oviducal eggs and there was no distension of contralateral oviducts to suggest monoallochronic laying, thus representing a major difference in this subspecies over its geographic range.

The endemic Western Australian 2n=34 race of *P. m. marmoratus,* displays a markedly different male reproductive pattern from *P. m. alexanderi.* The testicular volumes were maximal over the spring-early summer period (Figure 2) and corresponded with maximal levels of gravid females (Figure 1). However gravid females were also recorded in winter (May-June) indicating fertilisation at a time corresponding to low testicular volumes. All gravid females collected during winter occurred on islands off the southern coast and there was little temporally comparative data from the adjacent mainland.

The information available on the highly localised 2n=32 race was sparse but indicated gravid females in spring. D. King (pers. comm.) collected seven visibly gravid 2n=32 females in a sample of 40 on 3 November 1979; two eggs were seen in four individuals and a single egg in the remaining three. The pattern of the reproductive cycle in both sexes of this race remains conjectural.

Both the 2n=34 and 2n=36 race of *P. marmoratus* in south-western Australia showed evidence of seasonal sequential clutching with individual females possessing both oviducal eggs and enlarged ovarian follicles (Figure 1). Females of both races also showed a peak of reproductive activity in the spring-early summer, a pattern characteristic of geckos in winter rainfall areas of south-western Australia (How and Kitchener 1983; How, Dell and Wellington 1986). The occurrence of gravid 2n=34 females during winter could reflect a response to favourable rainfall in autumn; a response similar to that documented for summer rainfall in the diplodactyline geckos of the subgenus *Strophurus* (How, Dell and Wellington 1986). Over 30% of females in both races had a single oviducal egg and several had only a single developing ovarian follice; suggesting a high proportion of single egg clutches.

Despite the inadequacy of monthly male samples, there was a pronounced difference in the male cycle between the 2n=34 and the 2n=36 races, the former having significantly greater testicular volumes in spring (September-October) and lesser volumes in autumn (May). The pattern determined for 2n=36 males in this study is in general agreement with that for this race in South Australia (King 1977), however, 2n=34 males have a pattern characteristic of spring breeding geckos (How and Kitchener 1983; How, Dell and Wellington 1986).

Most 2n=34 females were gravid during the period of highest testicular volumes (August-December), consequently, there is no evidence to suggest overwinter oviducal sperm storage by females in this race. It is possible that sperm storage occurs however, as some females were gravid during winter (May and June) when male volumes are lower. This anomaly is in need of a detailed histological examination in an area of parapatry to determine if reproductive patterns in the 2n=34 and 2n=36 races are sufficiently divergent to suggest the subspecies are reproductively isolated and hence species.

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