Growth of an Australian Murid (Pseudomys novaehollandiae) in the Wild

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Specimens of *Pseudomys novaehollandiae* (Waterhouse, 1843) were live-trapped for dissection (1972—74) and capture-mark-release (1974—76) studies in central coastal New South Wales, Australia. Body weights of single and multiple capture animals less than 1 year old are used to describe growth under natural conditions. Variations in growth rate are related to (1) time of birth within the breeding season (early- or late-born cohorts) and (2) rate of sexual development (mature or immature during the season of birth). Animals which matured grew more quickly than those which remained immature until the following season. As a group, mature individuals reached a higher asymptotic weight (16.4 g) than immature individuals (14.9 g) and attained 90% of this asymptote at a younger age (60 days compared to 75 days). Individual growth records showed that this difference in growth rate only became apparent after 50 days of age. Although the early-born cohort grew more rapidly than the late-born, the difference was minimal if mature animals were excluded from the analysis. Final body weight and overall growth pattern were similar under field and laboratory conditions except that laboratory animals weighed more when under 30 days of age.

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I. INTRODUCTION

The first rodents to colonise Australia were probably the ancestors of the present-day pseudomyines (S i m p s o n, 1961), an endemic group of *Muridae* to which the genus *Pseudomys* belongs. This group now includes a diversity of forms, some of which resemble the voles, gerboas and typical rats and mice from other parts of the world. The pseudomyines, together with other murids which arrived in Australia later, are found throughout the continent and in most habitats. Broadly speaking, the biology of Australian rodents is related to wheather they occupy the dry inland regions (desert and semi-desert species) or the more moist coastal belt (non-desert species). Desert and semi-desert species are generally opportunistic breeders and experience wide fluctuations in population size depending on environmental conditions N e w-

s o m e & C o r b e t t, 1975). Non-desert species are either seasonal or year-round breeders and their populations are more stable from year to year. Although very little is known about the growth rates of wild rodents in Australia, a comparison of several species raised in the laboratory showed that opportunistic and short-season species usually grow more rapidly than long-season or year-round breeders (K e m p e r, 1976a).

Pseudomys novaehollandiae is a non-desert species found in south-eastern, coastal Australia where winter (June-August) are generally cool and wet and summers (December-February) are hot and dry. In wild *P. novaehollandiae* there is a well-defined breeding season which is usually 4—5 months long but laboratory animals will breed all the year. During the first 3 years of the present field study, births were recorded between September and early January (spring-early summer) but in the fourth year exceptional circumstances resulted in a much longer season and births occurred from October to March (K e m p e r, 1977). Both sexes become sexually mature in the season of their birth but normally this is only possible for some of the early-born (September-October) individuals. Wild females reach maturity as early as 7 weeks after birth when 12 g or more in weight. Laboratory females mature between 7 and 23 weeks (11—20 g) and laboratory males between 11 and 36 weeks (about 14 g) (K e m p e r, 1976). Growth and development studies showed that weaning occurs at 3—4 weeks, adult weight is 16 g and there is no sexual dimorphism in body weight in growing or adult animals (K e m p e r, 1976a).

In this paper, growth rate variations of wild *P. novaehollandiae* are described and discussed in relation to time of birth and rate of sexual development. The growth patterns of wild and laboratory *P. novaehollandiae* are also compared.

II. MATERIAL AND METHODS

Two trapping studies were carried out in the Nelson Bay-Smith Lake region of New South Wales, Australia (32°26'—45'S., 152°00'—28'E.). In the first, animals were live-trapped then killed and dissected (May 1972—May 1974) and in the second, animals were marked and released (*CMR*) on a 3 ha study plot (August 1974—July 1976). Trapping was carried out for 2—5 nights, usually at monthly intervals. Sherman-type aluminium live-traps were used throughout and on two occasions during the dissection study they were supplemented with break-back mouse traps. A peanut butter-rolled oats mixture was used as bait for the first, third and fourth years, cotton wool soaked in linseed oil during the second. *CMR* animals were marked by toe-clipping.

Dead animals were weighed with a torsion balance to 0.1 g and live animals were weighed in a cloth bag with a spring balance graded in 0.5 g units. Body weights

of *CMR* animals were averaged for each trapping period. Weights of pregnant females were adjusted to a non-pregnant weight by subtracting the estimated amount of gain due to pregnancy (K e m p e r, 1976b). This non-pregnant weight was then recorded at the estimated age or date of conception.

Females were considered mature if the vagina was perforate or if they were pregnant or lactating. Live males were regarded as mature if the scrotum was distended. Dead males were classified as mature if the testes were found to be spermiogenic and the accessory glands enlarged. In this paper the terms mature and immature also refer to the reproductive history of an individual *i.e.* whether or not it was known to have matured in the breeding season in which it was born.

Animals were aged using a combination of methods. Amount of molar wear was used to separate the two age classes of 0—1 year and 1—2 years (K e m p e r, 1977). Body weight and measurements, cranial measurements, eye lens weight and stage of post-juvenile moult were used to give a more precise age (in days *postpartum*) to animals that were obviously young.

A generalised growth equation ($Y = \alpha + \beta \varrho^x$) was used to describe all curves for wild animals. The curve for laboratory animals was constructed using the five-point floating average method with data from 110 young (K e m p e r, 1976a). Growth of the early- and late-born cohorts (Fig. 1) was compared using the mean body weights of six 5-week periods for each cohort and a Student's *t* test. Growth of mature, early- and late-born immature animals (Fig. 2) was compared using the mean body weights of four age periods and a Duncan's Multiple Range test (Table 1).

III. RESULTS AND DISCUSSION
1. Growth, Time of Birth and Sexual Development

Growth curves for the early- and late-born cohorts are illustrated in Fig. 1 by plotting body weight against date of capture for all animals from the dissection and *CMR* studies (*i.e.*, single and multiple capture individuals). Although breeding was extended until March in the fourth year of study only one juvenile was captured whose estimated date of birth fell outside the normal September — early January season. For this reason, data from all years could be combined and early-born (September—October) and late-born (November—early January) could be defined in the same way.

The early-born cohort grew more quickly because it reached its asymptotic weight faster than the late-born (Fig. 1). Assuming that the origin of each curve (6—7 g) represents animals of roughly the same age, the cohorts can be statistically compared using the mean body weights of corresponding 5-week periods for each cohort. The results showed that early-born animals were significantly heavier ($P < 0.05$) during the first two periods but not thereafter. A comparison of consecutive means within the same cohort showed that the early-born stopped growing after the third period but the late-born did not stop

growing until after the fourth. These comparisons, which indicate faster growth in early-born animals, may not be valid if the assumption of equal age at the curves' origins is incorrect. Furthermore, it is possible that the large number of mature animals, which were generally heavier than the immature, affected the growth pattern of the early-born.
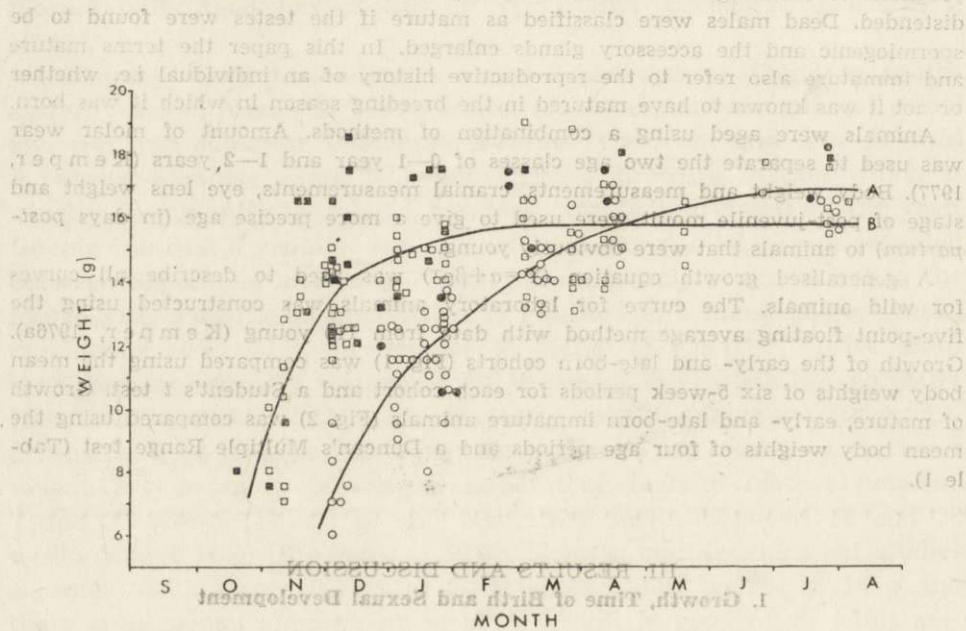

Fig. 1. Growth of early-born (B) and late-born (A) wild *P. novaehollandiae.* Body weights of early-born mature (■) and immature (□), and late-born mature (●) and immature (○) are plotted against date of capture.

In view of the fact that growth rate and sexual development may be closely related, the body weights of mature, early-born immature and late-born immature animals were plotted against age (Fig. 2). Mature animals had the most rapid growth rates and reached 90% of asymptotic weight (16.4 g) at 60 days. The early-born immature group also reached the 90% level at 60 days but their asymptote was considerably less (14.5 g). Late-born immature animals did not reach 90% of their final weight (15.4 g) until 90 days. Comparison of the mean weights of the three groups at four age periods showed that mature animals were significantly heavier than immature animals at ages greater than 50 days (Table 1). Immature early- and late-born were significantly different at 51—70 days only.

The different asymptotic weights reached by early- and late-born animals in Figs 1 and 2 do not reflect real differences in maximum body

weight. In both cases there was no significant difference ($P > 0.05$) when means were compared. The higher asymptote of mature animals (Fig. 2) was, however, significant and is supported by other observations. Parous

Table 1

Results of a Duncan's Multiple Range test performed on the body weights of mature (A), late-born immature (B) and early-born immature (C) *P. novaehollandiae* in four age periods. Underlined letters indicate no significant difference. $* = P < 0.05$, $** = P < 0.01$. Letters are ranked with highest value at left.

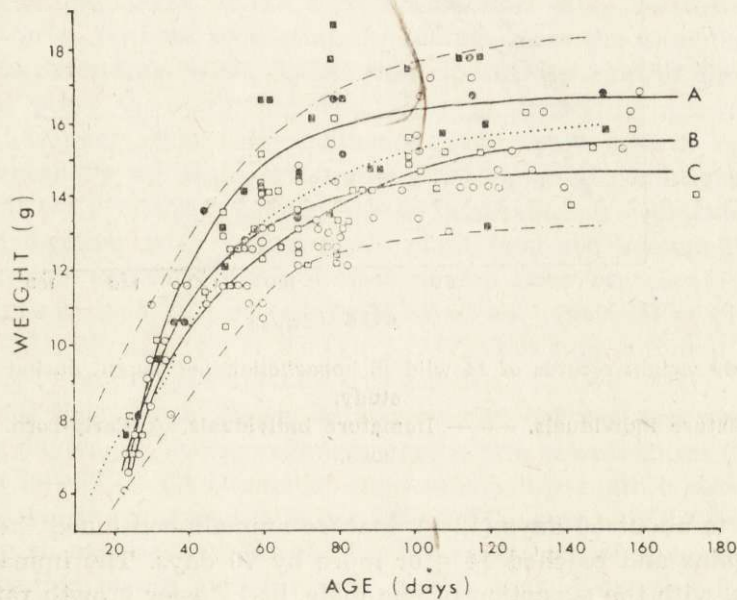| Age (days)			
20—50	51—70	71—90	91—180
	**		**
A C B	A * C ** B	A ** C B	A * B C

Fig. 2. Comparison of growth of wild (——) and laboratory (......) *P. novaehollandiae*. A — Mature. B — Late-born immature. C — Early-born immature. Symbols represent wild animals only and are the same as Fig. 1. 95% confidence limits (·—·—) included for laboratory animals.

females are known to remain heavier than the rest of the population for several months after breeding has ceased. Also, immature animals experience a marked lull in growth during winter and do not normally

attain adult weights (16 g) until just before breeding begins (K e m p e r, 1977). These patterns have been observed by B e r g s t e d t (1965), W a r n e k e (1971) and B u j a l s k a & G l i w i c z (1972) in other rodents.

Further evidence of the relationships between growth rate, time of birth and rate of sexual development comes from the body weight records of 14 *CMR P. novaehollandiae* of known cohort and reproductive status (Fig. 3). Mature and immature individuals had similar growth
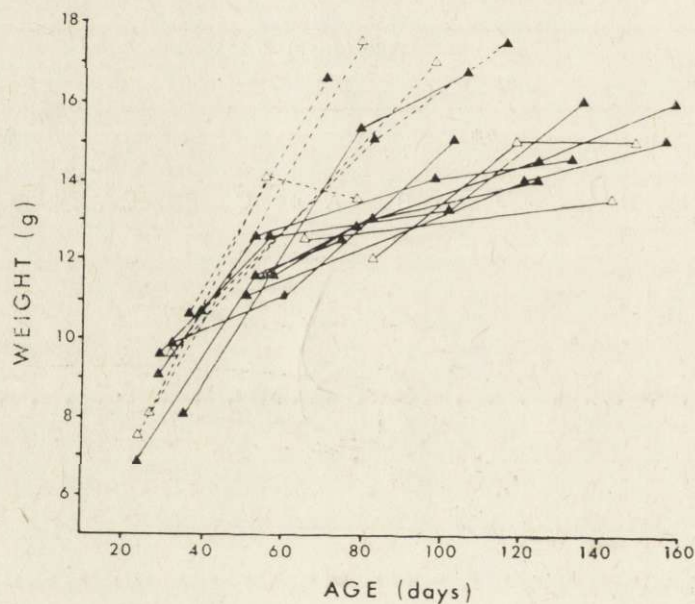

Fig. 3. Body weight records of 14 wild *P. novaehollandiae* caught during the *CMR* study.
— — — Mature individuals. ——— Immature individuals. △ Early-born. ▲ Late-born.

rates up to about 50 days (12 g). Mature animals continued their rapid weight gains and reached 14 g or more by 70 days. The immature individuals, with the exception of one male, had slower growth rates after 50 days and did not reach 14 g until at least 100 days. Similar results were obtained by Z e j d a (1971) who found that growth rate differences between mature and immature *Clethrionomys glareolus* became apparent after 2 months of age. In the *P. novaehollandiae* illustrated in Fig. 3, growth rate did not appear to be related to time of birth within the breeding season. Early-born animals grew slowly if they did not mature and late-born grew quickly if they did mature.

A close relationship between growth rate and sexual development is

predictable in animals which mature in the breeding season of birth. Rapid growth is required in order to reproduce before the end of the season, especially in species with short breeding seasons such as *P. novaehollandiae*. All wild *P. novaehollandiae* were at least 12 g when they reached sexual maturity and most were over 14 g. Immature animals generally weighed less than 14 g but there were some early-born individuals which reached 14—15 g well before the end of the breeding season (Fig. 1). The attainment of adult, or near adult, size is therefore not necessarily coincident with that of sexual maturity. There must be other factors operating to suppress early maturation in some members of the population.

In several European rodents it has been shown that the early-born cohorts grow more quickly than the late-born (S c h w a r z *et al.*, 1964; B e r g s t e d t, 1965; M a r t i n e t, 1967; S a i n t G i r o n s, 1967; M a r t i n e t & S p i t z, 1971; B u j a l s k a & G l i w i c z, 1972; A d a m c z e w s k a - A n d r z e j e w s k a, 1973). In these species, however, a large proportion of the early-born cohort often matures in the season of birth. Without separating the mature from the immature, it is difficult to determine which factor, time of birth or rate of sexual development plays the more important role in regulating growth rate. In fact, it is likely that early maturation and rapid growth rates are both enhanced by the same favourable environmental conditions which are present early in the breeding season. Increasing, or constantly long, daylength together with young, green plant food are known to result in rapid growth and early maturation in several rodent species (Y o u n g, 1965; P i n t e r, 1968; M a r t i n e t & M e u n i e r, 1969; M a r t i n e t & S p i t z, 1971; M e u n i e r & S o l a r i, 1972) but high ambient temperatures (33°C) retard growth (D a k e t s e & M a r t i n e t, 1977).

In coastal New South Wales, September and October are months of increasing daylength, spring vegetation and warm temperatures (average maximum 20—25°C). By December and January daylength is decreasing, the vegetation is spent and it is hot (25—30°C) and usually dry. It is reasonable to assume that the favourable conditions of the early part of the breeding season enhance rapid growth and maturation in early-born *P. novaehollandiae*. Clearly, if these were the only environmental factors affecting growth and sexual development, all early-born animals would grow and mature quickly but this was not the case. The fact that population density may be important was indicated by observed differences in the proportion of young females maturing in the season of their birth (K e m p e r, 1977). In the first *CMR* breeding season density was low and 88⁰/o of the young females matured but in the second season density was higher and only 37⁰/o matured. Growth rates were

slower in the second year. Retarded growth and sexual development,
are characteristic of high population densities in many rodents (C h r i-
s t i a n, 1971), and it appears that the same may be true of *P. novae-
hollandiae.*

2. Comparison with Growth in the Laboratory

A comparison of growth in laboratory and wild *P. novaehollandiae*
showed that the pattern was similar in both environments (Fig. 2). Most
body weights of wild animals fell within the 95⁰/₀ confidence limits set
by the laboratory population and the asymptotic weight of laboratory
animals was between those of mature and immature wild animals.
Since most laboratory animals were sexually mature by 150 days it is
surprising that their asymptotic weight was not closer to that of mature
wild animals. A possible explanation for this is that parous females,
which are heavier than non-parous females (even after the weight gain
due to pregnancy has been subtracted), were excluded from the labora-
tory curve. Growth rate, in terms of the age at which 90⁰/₀ of asymp-
totic weight was reached, was almost the same in laboratory (85 days)
and late-born immature animals (90 days).

The one obvious difference which was noted in growth between the
two environments was that laboratory animals were heavier at ages less
than 30 days. The smallest *P. novaehollandiae* trapped in the wild were
6—7 g. At this weight laboratory animals averaged 15 days, the day
when most young opened their eyes (K e m p e r, 1976 a). Semi-inde-
pendence, and therefore trappability, would be unlikely in wild animals
at this age. It is assumed that laboratory conditions resulted in higher
body weights in young animals, a conclusion also reached by B u j a l-
s k a & G l i w i c z (1968) when studying *Clethrionomys glareolus.*

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TEMPO WZROSTU U *PSEUDOMYS NOVAEHOLLANDIAE* W TERENIE

Streszczenie

Badania tego australijskiego gatunku gryzonia myszowatego prowadzono w Nowej Południowej Walii. Zwierzęta były łowione żywe do badań sekcyjnych (1972—1974) lub były łapane a następnie po zaznakowaniu wypuszczane (1974—1976). Podstawą oceny ich wzrostu w warunkach naturalnych były pomiary osobników łowionych jednorazowo lub wielokrotnie, w pierwszym roku życia.

Zróżnicowanie tempa wzrostu zależy od: (1) okresu urodzenia (wczesna lub późna kohorta — Ryc. 1) i (2) tempa osiągania dojrzałości płciowej (tylko część dojrzewa w sezonie urodzenia). Osobniki które dochodzą do dojrzałości płciowej rosną szybciej w porównaniu do tych, które stają się aktywne płciowo dopiero w drugim kalendarzowym roku życia. Należy przy tym podkreślić, że różnice w ciężarze zaznaczają się u osobników w wieku ponad 50 dni. Chociaż zwierzęta urodzone we wczesnych kohortach rosną szybciej niż osobniki z kohort późniejszych to różnice stają się znikome jeśli nie bierze się pod uwagę osobników dojrzewających płciowo jeszcze w tym samym roku (Tabela 1). Ciężar ciała i tempo wzrostu było u zwierząt trzymanych w warunkach laboratoryjnych podobne jak u żyjących na swobodzie, choć w laboratorium są one w pierwszym miesiącu życia nieco cięższe (Ryc. 2).