

THE RODENT GENUS PSEUDOMYS IN THE ARID ZONE

① This paper will address the question of the biology and conservation of the rodent genus Pseudomys which presently comprises 19 described and two undescribed species and is the largest genus of Muridae in Australia.

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Since their arrival in Australia 5-10 million years ago, the distribution of Pseudomys species has been influenced by climatic change, the burning and hunting practices of aboriginal man, and now finally by the various effects of European settlement.

The present distributions of the 18 extant species of Pseudomys suggest that it is unusual for two or more species to be found together. Exceptions to this generalization include P. delicatulus and P. nanus which are often recorded together in the Kimberley, P. albocinereus and P. praeconis occur together on Bernier Island, and P. australis, P. hermannsburgensis and P. desertor overlap to some extent in inland arid areas.

However, Pleistocene and Recent fossil deposits suggest that it was common for two or three species to be found together and although it is difficult to be certain that they actively co-existed at any one time, it does suggest greater overlap of their distributions in the past. More recent sub-fossil deposits indicate that P. hermannsburgensis, P. shortridgei, P. praeconis and P. desertor probably co-existed on Dirk Hartog Island, and that P. albocinereus, P. occidentalis, P. shortridgei and P. praeconis were present in the Jurien district prior to European settlement.

Thus it appears that the Pseudomys species, like other Australian rodent species, had more extensive distributions than at present. Many appear to have begun their decline prior to European settlement and reasons such as increased aridity, sea level changes and the influence of aboriginal man through hunting and use of fire, have been proposed for this decline.

Increasing aridity and reduction of forested areas over the last 40,000 years possibly contributed to the reduction in range of

the three mesic species P. higginsi, P. fumeus and P. oralis and the extinction of another undescribed species of Pseudomys from western Victoria.

Since European settlement in Australia, possibly two species of Pseudomys have become extinct and another five species have continued to reduce their distribution. Conservation of this rodent genus necessitates, not only a knowledge of the present conservation status of the species, but also a knowledge of their requirements which then leads to an understanding of the reasons for their past and present distribution.

In this paper, I will initially discuss the general biological characteristics of the genus, and then look at patterns of decline of groups of species of Pseudomys in certain regions of Australia.

The majority of Pseudomys species occupy, or did occupy arid and semi arid regions, and only three species P. higginsi, P. fumeus and P. oralis could be regarded as having mesic distributions. Within these broad regions these native rodents are restricted to uncleared land and do not show the capacity to immediately invade disturbed areas as do Mus musculus. However some species, such as P. novaehollandiae return to revegetated areas following mining, and others, as we will see, require certain fire regimes for survival.

Many species occupy wide ranges of habitats in these areas. For example, P. fumeus is found in mountain habitat as well as coastal dunes in Victoria, P. delicatulus and P. nanus are found in sandy plateau woodlands, river fringing vegetation, valley woodlands, and rugged boulder country in the north west, and P. hermannsburgensis is recorded from low woodlands on sandy soil, sand ridges, and gibber plains. Other species such as P. occidentalis, P. oralis and P. arborum are restricted to specific vegetation or soil types.

Since most species of Pseudomys occur in arid or semi arid habitats, it is not surprising that biological studies have concentrated on species from these areas.

Survival in these areas depends on the interplay between the physiology and behaviour of an animal and the performance of some Pseudomys species in these aspects is comparable to the much studied Notomys alexis. Under conditions of reduced water availability in the laboratory P. australis and P. hermannsburgensis are able to reduce their total water requirements by up to 60% through a reduction in evaporative water loss; a reduction of up to 90% of urine volume, an ability to concentrate urine to a high degree, and reduced faecal water loss. Many are capable of surviving on seed alone in the laboratory.

However in the field, Pseudomys, like other Australian rodent genera, utilize a wide range of dietary items and complete granivory is not known. P. apodemoides eat seed, fruits leaf and stem, as well as fungus, lichen and insects. P. nanus and P. gracilicaudatus are almost exclusively grass and grass seed eaters, while P. australis and P. desertor utilize seed, green plants and insects in their diet. Studies on P. albocinereus have shown that insects in the diet are important for maintaining water balance during the summer months.

It would therefore appear that the urine concentrating ability of these species is not related to a shortage of water in the diet, rather than to compensate for the increased evaporative water loss required for activity in the field.

Pseudomys are predominantly seasonal breeders, although some species exhibit the capacity to breed throughout the year provided conditions are suitable. In post fire regenerating heathlands P. apodemoides breed all year round, however in mature heathlands, females are highly seasonal in their reproduction. This seasonality in breeding is related to the flowering peak of the vegetation and seasons are not necessarily the same for two separate populations of P. apodemoides. The arid zone species P. australis

and P. hermannsburgensis respond to irregular vegetation flares and increase their numbers significantly although populations do not approach the plague proportions sometimes exhibited by Mus musculus and Rattus villosissimus. P. albocinereus as Jurien breeds only during the spring months and maintains relatively constant population numbers, while more widely distributed populations appear more opportunistic in their breeding pattern. In the Kimberley, P. nanus and P. delicatulus give birth throughout the year, although there is reduced reproductive activity towards the end of the dry season.

Most species have a gestation period of 28-31 days, an oestrous cycle of 7-10 days and litter sizes of 2-5. P. nanus has adopted a reproductive strategy of rapid development and reduced parental care with an oestrous cycle of 5-6 days, a gestation period of 22 days and the young weaned by 21 days.

Most species of Pseudomys are social especially during the breeding period and aggregate in their cool, humid burrows. This behaviour further aids water conservation. Species that do not occupy burrows, such as P. praeconicus and perhaps P. albocinereus in some areas, live in tunnels and nests beneath dense tussock grasses. Species that live in arid forested areas such as P. higginsii nest in rotting stumps and under leaves.

INLAND PLAINS

The major reductions in range of Pseudomys species has occurred predominantly among species inhabiting the inland plains of the southern half of the continent.

Of these, the inland plains of eastern Australia, including the Liverpool Plains of N.S.W., which were in permanent flood and the area around the Murray-Darling River junction have probably been exposed to European settlement and impact.

The Blandowski expedition to the region of the Murray-Darling River junction in 1856-7 recorded P. hermannsburgensis, P. gouldi and P. desertor. All are now believed extinct in this area, as are many other small to medium sized Pseudomys species.

P. gouldi and P. australis were recorded from the Livermore River in 1831, and have now disappeared. P. hermannsburgensis, P. australis and P. desertor have contracted their range to the more arid interior of Australia, while P. gouldi has become extinct throughout most of its range. P. gouldi was also recorded from the Moore River in W.A. in 1845 and sub-fossil remains from the Flinders Range suggest it was sympatric with P. australis, P. desertor, and P. hermannsburgensis in this area. Mus musculus remains were also present in these deposits and it would appear that the decline of P. gouldi throughout its range has only occurred in the last 100 years or so. There is a W.A. Museum record of P. gouldi from Mundrabilla in 1969, however some taxonomic confusion with P. australis exists in the Nullabor region.

Pastoralists entered these areas in the 1850's and the native vegetation upon which the rodents depended for shelter and food was heavily grazed. The grasses were closely cropped and much of the mallee scrub was cleared for wheat growing or burnt to clear land for grazing. The effects of overgrazing by sheep and the clearing were compounded by the introduction of the rabbit and the severe droughts of the 1880's. Many of the small mammals including the Pseudomys apparently could not tolerate the degradation of the habitat and potential for increased predation, and disappeared. P. australis is known to occupy only shallow burrow systems and the physical effects of stock trampling probably also contributed to the decline of this species. The larger size of P. gouldi (approximately 50g) may have contributed to this species decline through its range as a result of increased predation following habitat alteration. Smaller species with which it was previously sympatric such as P. hermannsburgensis and P. desertor still survive in some areas.

WHEATBELT

Six species of Pseudomys have been recorded in the wheatbelt, and three of those, P. desertor, P. hermannsburgensis and P. gouldi are now extinct in this area. P. nanus occurs elsewhere in Australia, and, as mentioned previously, P. gouldi is probably extinct throughout its range.

The decline of many small and medium sized mammals in the wheatbelt was observed by Shortridge, in the 1880's prior to any extensive grazing or clearing, and introduction of foxes, and rabbits.

It has been suggested that the mammals that have become extinct in the wheatbelt were those unable to cope with the alteration in environmental patchiness caused by changes in the patterns of fire resulting from European occupation.

H. shortridgei was last collected in the southern wheatbelt in 1931, but has since been rediscovered in western Victoria. It has been demonstrated that this species, as well as P. novaehollandae, and H. apodemoides require the presence of a number of plant species within their heath and shrubland habitat and the regular presence of these is dependent upon a specific fire regime. Dietary studies indicate that these species utilize a wide range of foods and the fire related seral stage provides the necessary diverse and predictable food supply.

The implication of this relationship between vegetation succession and the presence or absence of these neodomy species is that small populations will become extinct as local patches of vegetation mature. If suitable adjacent habitat is unavailable, they cannot disperse successfully and more will become extinct.

The optimum situation for the continued survival of these species appears to be a habitat mosaic of differing maturity subject to disturbance by fire which repeatedly initiated seral succession stages in the mosaic. Evidence suggests that pre-European history was in fact a mosaic pattern with the aboriginals systematically burning areas and promoting patchiness in the habitat. Following European settlement, extensive burning on a regular basis would have reduced large areas of the wheatbelt to a similar seral stage and species such as H. shortridgei which required the patchiness of the environment would have been adversely affected. Land clearing, introduction of foxes and predators would have exacerbated a further decline in their numbers.

P. shortridgei was last collected in the wheatbelt in 1940, foxes were well established. It was suggested earlier that some species occupying arid zones declined while surviving in more mesic areas. This may apply to P. shortridgei.

The other two species of Pseudomys which have now disappeared from the wheatbelt, P. nanus and P. Gouldi were only recorded from Moore River on the western edge of the wheatbelt in 1940. Presently P. nanus is relatively common on narrow island in Spinifex and Triodia habitats and throughout the Kimberley in habitat consisting of variable shrubs over hummock and tussock grasses. Dietary studies suggest that P. nanus predominantly eats native grasses and any change in the abundance of these grasses may have contributed to the demise of this species in the Moore River area. P. Gouldi may have also depended upon native grasses for its continued survival both at Moore River and on the grasslands in eastern Australia. Pastoral leases were taken up in the Moore River area in the 1850's, and the grassland habitat probably would have been the first to be modified by this activity.

While referring to the extinction of rodents from the Moore River area it is relevant to mention that Notomys macrotis and N. longicaudatus were also collected in this area in the 1840's, and are now extinct. These species, and P. Gouldi were all in the 50-100g weight range and the role of the cat in the extinction of these rodents should not be overlooked.

There is a record of a dasyurid Macrotis (30-50g) being killed by a cat at Williams in 1941 and it is likely that cats were present with the first pastoralists in the Moore River area, and possibly contributed to the decline of these rodent species. Macrotis was collected in the Moore River area in 1840, and these too are now extinct. Decline of these larger rodents.

The surviving species of Pseudomys in the wheatbelt are P. occidentalis and P. occidentalis appear to have survived in the same associations as before.

The present known distribution of L. occidentalis is from eight locations in the southern wheatbelt, although fossil and sub-fossil deposits suggest a wider distribution which began contracting prior to European settlement. More recent surveys indicate that this species is probably not as rare as initially thought. The preferred habitat for this species appears to be mid dense shrublands which have not been burnt for at least 10 years. The conservation of this species depends on the preservation of large areas of such vegetation so that in the event of fire suitable alternative habitat is available for colonization. Reserve size of at least 2,000ha would appear necessary for this species' survival.

L. albocinereus does not appear to have reduced its overall distribution at all either prior to, or following European settlement. This species prefers heath and shrublands that have not been burnt for at least six years, and is capable of surviving in areas of uncleared habitat as small as 500ha. This is possibly due to the nature of fires in its preferred habitat, that is fires are not extensive and leave suitable unburnt patches in smaller total areas. This is in contrast to the habitat of L. occidentalis which tends to support more extensive fire patterns, thus necessitating larger areas of habitat for individuals to 'escape' to.

The ability of L. albocinereus and L. occidentalis to utilize a wide range of dietary items would further enhance their ability to tolerate the effects of European settlement. Dietary specialization would be disadvantageous in a changing environment.

RESTRICTED DISTRIBUTION

Apart from L. occidentalis, there are two further species of Pseudomys which have very restricted distribution in Australia and whose conservation critically depends upon the preservation of habitat.

The Shark Bay Mouse L. praeconia was originally found on the Marion Peninsula, Shark Bay in S.A., now very rare.

specimens have come only from Bernier Island where it is fairly common. Sub-fossil remains from Mid Pliocene, and Jurien and fossil finds in the upper Pleistocene of Western Desert suggest a much wider distribution until 150,000 years ago.

The habitat of this species on Bernier Island is dense Spinifex longifolius and Cleoria axillaris on coastal sand hills. There are no records of burrows for this species and it is possible that they depend on tunnels beneath dense spinifex tussocks for shelter. Diet is fairly specialized, consisting mainly of flower petals and anthers with some leaves and stems of fleshy plants. This species is a relatively slow breeder with an oestrous cycle of 14 days, nearly twice as long as most Iseidomys.

The successful conservation of this vulnerable species would appear to rely on the preservation of a mature vegetation association to provide the specialized breeding and dietary requirements of this species. The introduction of foxes or cats would be disastrous for this species, and the elimination of goats from Bernier Island would be beneficial to this species.

The Hastings River Rat I. oralis is regarded as one of the rarest Iseidomys and is known from only a few localities in N.E. Queensland. Before 1969, I. oralis was known from only two specimens collected in the 1840's from the Hastings River district in N.E.W. It was rediscovered in 1969 in habitat of bracken covered creek beds in open casuarina woodland. Extensive trapping since 1969 has revealed the presence of a few scattered colonies in suitable habitat, however it is not known from any national park or reserve. Virtually nothing is known of the biology of this species, however its restricted distribution suggests that habitat fragmentation even on a small scale would lead to the extinction of this species.

CENTRAL ARID

Many species of mammal in the central arid regions of Australia have also undergone drastic changes in their distribution and status since European settlement.

Twelve species of rodent, including four Macrotomys, have been recorded from this region. Four species, M. fieldi, Macrotomys apicalis, Notomys amplus and M. longicaudatus are now believed extinct and only four species could be considered as not having reduced their distribution significantly since European settlement. Again it is the smaller rodents which do not appear to have declined to the same extent as the medium sized rodents and marsupials. The species of rodent now extinct in this region were all in the 70-150g weight range while two of the species that have not altered their distribution significantly Notomys alexis, M. hermannsburgensis are in the 15-40g weight range.

In the Warburton region, only the larger kangaroos and smaller rodents and dasyurids are now considered common. Eight species of medium sized mammal are believed extinct. Similarly, by 1970, 14 of the 29 marsupials from central Australia including most of the bandicoots, rat kangaroos and small wallabies had disappeared.

The extensive clearing and burning for agriculture which contributed to the decline of many species on the inland plains of eastern and western Australia did not occur in the central region. This region has, however, supported a cattle pastoral industry since 1872, and the vegetation particularly the grasses, on the preferred wooded sandplains and flood plain areas has been altered considerably. The vegetation of the desert dunefields, that is areas not grazed by cattle, has probably also been altered over the last 100 years or so. Aborigines long employed a temporal and spatial mosaic pattern of light winter burns to ensure a continuous supply of successional food plants and to assist in hunting. With the concentration of aboriginal population in a few settlements the timing, extent and frequency of fire would have changed so that now infrequent but intensive summer fires are more common.

Looking at the species from the central arid region individually, P. fieldi is known from only one specimen collected near Alice Springs in 1894, and this species' decline ^{continued} ~~must have occurred~~ very rapidly after European settlement. P. fieldi remains abundant in subfossil cave deposits in N.T. ~~is a very rare species in the central arid region~~
~~more abundant than in the central arid region~~
P. australis occupy river flats, claypans and gibber plains, that is areas preferred for cattle grazing. They also occupy shallow burrow systems and these would be susceptible to destruction by trampling. This species is unusual among Pseudomys as its distribution comprises temporary colonies. Reasons given for this fluctuation in population numbers in a given location include a natural decline in the moisture content of the diet following a vegetation flush, and predation by owls. With the introduction of cattle, and foxes and cats, this cyclic population increase and decrease would have been interrupted in some areas as the vegetation changed and predation pressure increased. Local extinction would have occurred and the species contracted its distribution to less disturbed habitats.

P. desertor has also been recorded from a wide range of habitat, but now appears restricted to undisturbed areas such as lateritic breakaways and ungrazed dunefield areas. Unlike P. australis this species tends to be more solitary and is not found in

colonies, and this behaviour may be partially responsible for its apparent low numbers when compared with other species such as P. hermannsburgensis and Notomys alexis from the same area.

P. hermannsburgensis has not contracted its range to any great extent since European settlement and it is now widespread from central Australia to the west coast. This species is gregarious and breeding is predominantly opportunistic following good rainfall.

This species was initially called the Pebble Mound Mouse, as this species was associated with burrows under mounds of pebbles has now been attributed to a newly described species P. chapmani. Based on the distribution of disused mounds, this species' distribution appears to have declined in the Pilbara, however reasons for this are not yet apparent.

TROPICS

Despite approximately 130 years of grazing by cattle, and the presence of eight species of feral mammal, the mammal fauna of the tropical north of Australia has remained relatively intact.

Four species of Pseudomys are known from the Kimberley.

P. nanus and P. delicatulus appear to be widespread and have been recorded from a variety of habitats including sandy plateau woodlands, river fringing formations and rugged boulder habitat in the S.W., northern and eastern portions of the Kimberley. Another as yet undescribed species of Pseudomys has been collected from several locations in the north Kimberley, and P. hermannsburgensis has been recorded from the more arid S.W. region.

There is no evidence to suggest that any of these Pseudomys species have declined in numbers since the advent of the pastoral industry in 1885. Some medium sized mammals have become extinct in the S.W. and eastern regions of the Kimberley, and this has been explained by the degradation of the riverine woodlands by regular burning and direct and indirect grazing pressures of stock in these areas. This is in contrast to the grassland country in the south of the continent where burning and grazing pressure has contributed to the decline of many smaller species including Pseudomys.

Fire in the Kimberley quickly promotes regrowth of native shrubs and grasses. P. nanus and P. delicatulus predominantly eat grass and grass seeds and being independent of free water are capable of surviving away from watering points about which most habitat destruction occurs. Many of the medium sized marsupials probably depended upon waterholes for their survival. As we have seen also, these Pseudomys are not restricted to only one habitat for their requirements.

Both P. nanus and P. delicatulus are preyed upon by the dingo and cat in the northern portion of the Kimberley however no detrimental effect of this has yet been reported. The ability to breed practically all year round and their small size would tend to counteract this predatory pressure.

conclusions

It is now very difficult (~~and impractical~~) to predict the present day distribution and status of the genus Pseudomys if European settlement had not occurred in Australia. It is clear however that since their arrival in Australia some 5-10 million years ago, Psuedomys have been subject to continuous habitat modification by natural processes, Aboriginal man and European settlement. Many species apparently began to decline prior to European settlement, however loss of habitat through a change in the fire regime, extensive clearing and pastoral activities has ~~certainly~~ contributed to the extinction of one species, P. gouldi, and the reduction in range of another five species.

It appears that many of the species that are now believed extinct either locally or throughout their distribution, became so very quickly after European settlement in the area. For example P. gouldi was collected at the junction of the Murray and Darling Rivers in 1856-57, approximately 20 years after European settlement, and from the Moore River area in 1845, just as grazing activities commenced. Similarly P. fieldi was last collected in 1894, approximately 20 years after the pastoral industry commenced around Alice Springs. To some extent these observations reflect the frequency of collecting in these areas, but also indicate that these species were extremely vulnerable to habitat change.

The role of introduced predators on the decline of Pseudomys species has probably not been as great as on some of the medium sized marsupials. Certainly predation would have compounded the effect of habitat degradation, and I consider it significant that the four species of Pseudomys that have not shown any distribution contraction either prior to or following European settlement i.e. P. delicatulus, P. hermannsburgensis, P. albocinereus and P. apodemoides, are all small rodents in the 6-30g weight range, while the majority of those species which have contracted their range are larger, 40-90g.

~~It is unlikely that the cat has been responsible for the extinction of any Pseudomys from larger islands and predation by dingo and cats in the Kimberley does not appear to have affected the distribution of P. delicatulus or P. nanus. Many of the mammal species now extinct in the wheatbelt began to disappear before the introduction of the fox or cat.~~

Owl predation has been implicated in the fluctuation in numbers of P. australis and sub-fossil deposits suggest that owls fed on many other species of Pseudomys as well. Aboriginal hunting and native cat predation of the now extinct undescribed Pseudomys species from Western Victoria has been proposed as a reason for this species decline.

Mus musculus is now widely distributed in Australia and occurs in both uncleared and cleared areas. However Mus has not been shown to compete detrimentally with native rodents. Mus tends to colonize fire disturbed areas earlier than P. albocinereus and P. novaehollandiae, and where Mus and P. novaehollandiae do coexist there is a strong dietary separation of the two, with Mus tending towards insectivory, and P. novaehollandiae tending towards granivory. Even during plague situations, Mus did not compete to the exclusion of native rodents, in the N.A. wheatbelt.

It is possible that Mus musculus plagues could introduce greater predator pressure on native rodents, as numbers of diurnal and nocturnal birds of prey increase during this situation.

On the positive side, European settlement has resulted in an increased knowledge of the genus Pseudomys. Distribution patterns both past and present are becoming more complete, and two new species, P. chapmani and P. pilligaensis have been described in the last five years. At least two more species are known but as yet undescribed. The increased interest in our native fauna over the last 20-30 years has also resulted in three species of Pseudomys previously thought to be extinct, to be rediscovered. I refer to P. novaehollandiae rediscovered near Sydney in 1967, P. shortridgei rediscovered in western Victoria in 1961, after being known previously from only S.W. Western Australia, and P. oralis rediscovered in 1969 after an absence of 120 years.

Our knowledge of the genus Pseudomys is far from complete. The requirements of species, especially those with restricted distributions such as P. praeconis, P. occidentalis and P. oralis must be known to enable reservation of suitable habitat. Detailed survey work must continue to complete our knowledge of distribution patterns of this genus.

In summary, it appears that Pseudomys species with very specific requirements and a larger size have been more prone to extinction and range reduction. The main causes of this would seem to be direct habitat degradation through the agency of clearing, grazing and fire, with predation playing a secondary role.

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