

BEHAVIOUR AND TERRITORIALISM IN *TRICHOSURUS VULPECULA* (MARSUPIALIA)

R. I. KEAN

Forest Research Institute, N.Z. Forest Service, Wellington

INTRODUCTION

In New Zealand *Trichosurus vulpecula* was first liberated about the year 1840 (Pracy 1962) and during the following century it became distributed throughout the greater part of the country. In 1953 research was begun primarily for the purpose of evolving practical methods for killing the animals on farm lands and in forests. The terms of reference precluded formal experimentation on fundamental aspects such as behaviour, but continued observations led to some tentative conclusions.

METHODS

A field station was established in indigenous forest of the Orongorongo Valley, near Wellington. Six outdoor pens were constructed. Four of these measured 16×16 feet, one 16×32 feet, and one 9×8 feet. All were 9 feet high, and floored with concrete. Vertical posts and horizontal connecting poles provided climbing facilities. Up to three opossums were kept in each of the main pens; the large one held juveniles and spare males. Resting boxes, 22×9×9 inches, inside measurements, were available in excess. Another pen, of the same dimensions as the smallest one, was situated in Wellington. It differed in that an aluminium roof and a shelf for holding resting boxes greatly increased the available surface area and also gave optional protection from rain.

Basic food was dried peas and wheat (both softened in water) and limited amounts of green leaves, apples, dates or jam.

Stock was either wild-trapped or born in captivity, and was subject to intermittent disturbance through inspection, measurement, and the taking of vaginal smears.

Free-living opossums surrounded the station. Many of these were earmarked by tattoo, and there was some interchange of captive and free animals. Free animals, in smaller numbers, also visited the town pen or its vicinity.

OBSERVATIONS

Captivity

Opossums required about two months to become adjusted to captivity, even though food might be accepted from the hand in as little as two days. Temperaments varied considerably and characteristics which were evident when each animal was first trapped did not become fundamentally changed by captivity. Most opossums tolerated confinement but a few showed little activity and soon died unless released. Others became neurotic. This state was characterised by some degree of emaciation, by avoidance of other animals and by quick restless movement, often in a figure eight. The figure was 7 to 9 feet long, and its precise form depended on the availability of space free from physical obstruction and from scent markings of other animals. One young female traversed a regular 8 on the floor in one corner of the pen. Another female of similar age utilised crossed poles which, by their positions, required the 8 to have one large loop and a small one. Another, middle-aged, female, which was very thin and had pronounced nervous hypertension, restricted herself to a single pole along which she marched rapidly to and fro. In most animals this type of movement might last for about an hour, or could be quite short, perhaps ceasing from relief of tension; but for this last animal, length of duration was not determined; any disturbance during daylight, such as a sudden noise, would cause her to dash from her box and begin pacing with unchanging rapid steps. After an hour or so of this behaviour, she was always caught, returned to her box and locked in. The pacing afforded no evident relief and it probably would have been continued until terminated by complete exhaustion. A contrary example was provided by another female, one of three held in a single pen. After removal of the other and larger animals, this opossum began to drip urine along the poles which she had previously used in "figure 8" behaviour. Nervous tension had not been acute and her routine had been to emerge at dusk, feed intermittently for about half an hour and follow this by "figure 8" movement. Subsequently, when in sole possession

of the pen, she began marking with urine immediately on emergence, with evident satisfaction and with feeding deferred for about two hours. Initially the "figure 8" work appeared to relieve nervous tension. It seemed to be an activity which permitted mental exclusion of the other animals. The behaviour which replaced it provided a more effective exclusion of the other opossums by elimination of their scents and the substitution of a personal one.

VOCALISATION

(a) *Social*

The best known call is a uvular *Wuh-uh-uh-uh-uh*. It begins loudly, with accent on the first syllable, and is gradually reduced in intensity. The final syllables vary in number and occasionally are omitted entirely. There may be some background clicks but these can be distinguished only at short range. An animal when calling usually occupies a prominent, elevated position and may evoke a response of similar form from another animal. As many as eight opossums calling intermittently might be grouped in the trees surrounding the Orongorongo pens. Occasionally, one animal would commence the call, and another one join in the *-uh-uh-uh-uh* sequence. Opossums in the pens seldom responded. The call is predominantly male, but not exclusively so. It is most common during the April-May rutting season but may be made throughout the year, increasingly from January. The youngest animal making the sound, or attempting to do so, was a male 9 months old still associated with its mother.

(b) *Aggressive*

A fairly high pitched and repeated *Aaaaaah* seems, by human analogy, to indicate anxiety, and its use by an opossum faced with overt or covert hostility strengthens this supposition, but the purpose of the call is clearly threat. This is shown in its frequent reinforcement by the threat posture, by retreat of an opposing animal and by actual attack in default of evasive action being taken by a potential opponent. It is not used to start aggression, but has the evident meaning of: "I will probably attack if approached more closely." The call may be heard in daytime when several opossums occupy one resting shelter, either in captivity or in the wild, and presumably results from movement by one of the occupants disturbing its fellows. Serious fighting does not usually follow. In captivity, an opossum penned with larger ones frequently enters its box during a period of general inactivity

(usually after midnight), extrudes its head, and, in a position of security, voices defiance, sometimes for hours. In such cases, where the possibility of action is remote, lack of reality in the threat is reflected by a slightly lower pitch.

A deep grunt indicates annoyance without the immediate likelihood of further action. It is provoked by disturbance, and, in the daytime, may be made by an adult male from within a resting box as a result of sounds from cleaning or repairing pens. In captivity, attack by an aggressive opossum is usually made silently; but willing combat by two evenly matched opossums, usually males, is accompanied by a variety of noises without any apparent set pattern; grunts and *Wuh* sounds predominate.

(c) *Reproductive*

Sexually-active males make clicking sounds which may be evoked by the presence of an oestrous, pregnant or lactating female. The same clicks are infrequently made by oestrous females.

(d) *Fear and pain*

An opossum caught in a jawed trap makes many sounds, struggles and may attack the trap but motivation seems to be too complex to permit analysis of vocalisation. Similarly, an injured opossum worried by a dog may make low *Aaaaah* sounds when bitten but it seems unlikely that a fall in volume and pitch would change a threat call to one indicating pain. More probably in this instance, injury and shock terminate physical resistance before vocalisation ceases. Pouch young give high pitched squeaks when separated from their mothers, and dependent juveniles may squeal, but no adult opossum that I have handled has given any call that I could attribute to fear or pain.

(e) *Feeding*

Enjoyment of food is indicated by "smacking the lips", a sound which induces another opossum, especially an offspring, to approach and investigate.

(f) *General*

Vocalisation may be fairly well standardised for definite situations but it is subject to many changes, in both captive and free animals. Ejaculated parts of calls seem to result from surprise without relation to significance of the full calls, whereas different combinations of parts probably result from indefinite or conflicting emotions.

GESTURES

Opossums frequently seem dull and unresponsive on short acquaintance. This impression results from their nocturnal habits and their

limited facial expression. Emotions are indicated primarily by ear positions. In a general state of alertness, the ears subtend an angle of about 100 degrees. In anxiety or perplexity the ears are raised almost vertically and produce a median longitudinal fold in the scalp which shows as a dark line through the approximation of the black tips of the guard hairs. In anger, pain, fear or pleasure the ears are extended laterally, with the light coloured ear tips (of grey opossums) visible from the front. Differentiation of these emotions then depends on position of the body and fore-paws, on voice or on movement, but an observer is seldom in doubt about interpretation. Irrespective of their elevation, ears are turned towards sounds perceived or expected.

In threat, the body is held in a semi-erect position and the fore-paws raised, with claws in a position for striking. In grey opossums the light upper surface of the paws is displayed. When possible, the hind paws and the tail hold a supporting branch firmly.

An oestrous female may hold the tail low, almost horizontally, and wag it from side to side.

SCENTS

Specialised glands produce scents: a sternal gland on the chest has a sweetish musky odour, and a pair of anal glands contain a white emulsion with a penetrating acid smell reminiscent of pickled onions. A second pair of anal glands, by analogy, should be scent glands but they secrete cells suspended in a clear viscid fluid, and seem to have no distinctive odour.

The sternal gland is made up of greatly enlarged sebaceous and apocrine glands similar in type to those of the general body surface (Bolliger and Hardy 1944). Hair of the sternal patch is oily and stained a rufous brown by the secretion (Fig. 1). It is rubbed on any new object placed in an opossum pen and even a familiar observer may be anointed nightly. When a captive opossum is released it marks its outward path at short intervals by pressing the chest gland against branches or other prominent features.

The anal (or paracloacal) glands were described by Bolliger and Whitten (1948). Histologically, both types of gland are sebaceous although their lining epithelia differ in some respects and in one type the cellular secretion does not liquefy. The cellular glands are usually bilobed. Each lobe has a separate duct which terminates near the rim of the cloaca. The odoriferous oil glands each have a single duct which discharges between the ducts



FIGURE 1. *Sternal gland, shown by stained hair on chest of elderly female.*

Photo by J. H. Johns.

of the cell glands and results in three pores on each side of the cloaca.

Urine also forms a scent but faeces have no observed social significance. Defaecation is not associated with any ritual; the action is so casual that it has the appearance of occurring without conscious volition, not interrupting other activities. No faeces are deposited in shelters.

The sternal gland is the one most commonly used. Its odour permeates shelters and can be detected along tracks, particularly in places where tree trunks are traversed.

Urine is found in the next greatest frequency. It had little significance in the main pens where some 20 opossums occupied 1,500 square feet in

a concentration which was unnatural for such animals. In these conditions, urine, like faeces, was voided without apparent regard for occasion or place; but in the segregated town pen some individuals placed urine deliberately according to two patterns. In the first, urine was shed copiously on the ground with a sinuous body movement resulting in a roughly sigmoid strip about 18 inches in length. In the other form, urine was dripped slowly from long cloacal vibrissae, and formed a continuous trail which extended along some 20 feet of horizontal poles but did not cover all available poles. Such marking was associated with some proprietary rights recognised by a marking opossum and by others with some variation.

Usually the captive opossums, although they urinated freely, rarely drank, except sparingly during hot weather; but a urine-dripping opossum would take up to 100 ml. of water nightly.

Similar urination patterns are common in the wild. The short strips are conspicuous on stones or on projecting roots near tracks but the longer arboreal trails are seldom visible from the ground.

The anal *scent* glands do not appear to be used often. The odour of this secretion is not very strong but is readily perceptible in small amount. I have not encountered it in the wild. The oily secretion is voided, together with urine and faeces, when an opossum is frightened, but such evacuations show only disorganisation. A protective function has been suggested, but predators are not known to have been repelled by the scent and domestic cats will even eat the glands. In the five instances where I have located the scent in pens it has been placed before the entrance of a shelter box occupied by an opossum with reason for feeling insecure. On the only occasion when I observed actual deposition of the scent, a vaginal smear had been taken for the first time from a stable young female 18 months old. She was somewhat disturbed but not frightened. When released from a sack she climbed to a perch and dabbed her vent on it, leaving some anal gland secretion. She then returned to her shelter box placing two more crescentic depositions within six inches of the entrance. Presumably the first deposition on the perch was misplaced because of confusion.

No function has been suggested for the anal *cell* glands. Bolliger and Whitten (1948) found that these glands, unlike their accompanying *oil* glands, secreted continuously and that their cells which were resistant to decay became incorporated with the urine. It is possible that the cells do have an odour which is perceptible to opossums; alternatively their durability might give an added per-

sistence to odour of deposited urine. Phosphates, carbonates and oxalates sometimes appear in the urine as a heavy white precipitate (Bolliger and Whitten 1940). Such excretion is intermittent and irregular in occurrence. It has not been fully explained although a somewhat similar heavy secretion by some rodents of arid lands has been commented on by Schmidt-Nielsen (1964). The white deposit may be very obvious on dark coloured bark, but it is probably related to metabolism and not relevant to behaviour.

Males are stimulated by an oestrous scent. Inconclusive evidence suggests that this is borne by the urine and not by anal glands, although



FIGURE 2. *Bark of Coprosma lucida taken as food. An inclined branch has been removed from the tree and viewed from its lower aspect.*

Photo by L. T. Pracy.

possibly the odour permeates the whole body. A male may follow a female during the whole of the lactation period and it seems most likely that the post-oestrous mild attractant is produced by the glands which line the pouch. Such glands are sebaceous (Green 1963).

BITE AND SCRATCH MARKING

Bark of some tree species is taken as food but discrete horizontal bites are usually social marks. Feeding results in removal of young bark from an entire area (Fig. 2) but in marking, separate horizontal bites are made in bark and in soft or decaying wood (Fig. 3). Such bites may be made in many places but they are most frequent in prominent positions near tracks, on flanges of trunks at

some 18 inches from the ground or other firm support. They do not appear to be invariably the work of one animal and may be kept renewed throughout a number of generations. A variation is found on fibrous bark, where narrow strips about $\frac{3}{8}$ of an inch long may be torn free for several inches above and below a bite. Scratches also are very frequent. Many of them would be made involuntarily but may be so conspicuous that they are likely to be recognised by opossums as minor indicators of community or individual significance.

An enigmatic feature is the "play" tree (Fig. 4). Such trees are soft-barked ones which are usually over-mature or dead. They serve no obvious direct



FIGURE 3. *Marking by horizontal bites in the soft bark of Hedycarya arborea.*

Photo by L. T. Pracy.



FIGURE 4. *"Play tree" (Podocarpus hallii). The lower bark has been worn away mainly by scratching. (Diameter 60 cm.)*

Photo by L. T. Pracy.

practical function and their incidence appears to be determined by the availability of suitable trees rather than by location of tracks, other amenities, or needs of opossums. The trees are used for many years but when readily accessible bark or semi-decayed wood has been worn away they are deserted. "Play" trees are absent from some locations because of wear or because trees of suitable type were never available but the lack has no apparent effect on social organisation.

SHELTERS

During daylight opossums usually rest in shelters. Favoured situations are hollow trees or thick clumps of epiphytes; but cover may be found on the ground, under logs, in thickets, or in holes. If daytime aggregations result in high local densities, some opossums may lie in exposed situations. Such animals represent a vulnerable surplus of population; in New Zealand they are not troubled by wild predators, but they are subject to climatic stress during winter. L. T. Pracy (personal communication) reported high mortality among opossums in poor shelters after a heavy snowfall in pastoral country during 1947; they died in their resting positions.

Shelters are not constructed but are frequently formed by the forcing out of a space in dense vegetation, with perhaps some shaping of soft soil. Winter (1963) reported that an opossum which slept above the ceiling of a house made a shallow depression in aggregate "softboard" and lined it with a sparse ring of green leaves. Such lining is very rare. The hollowing out of the "softboard" was possibly related to the nature of material rather than to shelter construction since captive opossums frequently bite the soft pine of their shelter boxes, usually in late afternoons, presumably as a diversionary activity. The resulting depressions may be formed on floors but are more usual on side walls although they have no utility in such positions.

A shelter is most usually occupied by a single animal (or mother and young) but more may be present. Well-used ones may be often unoccupied and Dunnet (1956) stated that the behaviour of opossums when released showed that all local opossums knew the situations of accessible shelters.

In captivity, three opossums in one pen may occupy all three boxes, or their distribution may be 2, 1, 0 or 3, 0, 0 without any set pattern either in association of animals or in use of the boxes. Similarly, choice of box by a single opossum seems equally unpredictable.

DISCUSSION

Schultze-Westrum (1965) described for the phalanger, *Petaurus breviceps*, a social system regulated primarily by scents which were effective at three levels of organisation and designated *Individualduft*, *Gruppenduft* and *Artduft* respectively. A similar system is followed in the present paper but the terms "individual", "group", and "community" are not restricted to scents, they are applied to all forms of social activity. In this usage "community" does not correspond to *Art*, but refers only to the members of the species whose activities could affect a given individual; it does not refer to the species as a whole.

Petaurus forms hierarchical groups; individuals have their own personal scents, but group scent derived mainly from high-ranking males permeates body surface of all group members. In pairing behaviour the female is marked by the frontal gland which is borne on the head of the male.

No such social groups are known for *Trichosurus*. Pairing is usually a transient phase with sexual activities leading to copulation rather than to the establishment of a lasting bond. There is no frontal gland. The single young leaves its mother before the end of its first year (Dunnet 1956; Kean 1967). Certainly, multiple occupancy of shelters occurs as the sharing of an amenity with low availability, particularly on pastoral lands where trees are few; but evidence from captivity suggests that sharing, even by two adults, indicates toleration rather than attraction. Sharing frequently amounts to aggression, as when one opossum forces its presence on another even though better accommodation is available elsewhere. Broom (1898) contrasted the solitary state of *Trichosurus* (except during the pairing season) with the continued association of the ring-tailed and great gliding opossums.

Territories do not appear to be shared. In Australia, Dunnet (1956, 1964) described patches of open eucalypt forest separated by grassland where males maintained territories averaging 7.5 acres and females occupied individual ranges of about 2.7 acres. Since the latter areas tended to overlap, sometimes extensively, they were not considered to be territories. Unsettled individuals termed transients brought population densities to an average of one adult to about four acres but one area of 8.5 acres held 8 adult residents, 3 males and 5 females.

The Orongorongo study area, in a complex, mixed forest, carried about 2.6 opossums per acre (Batcheler *et al.* 1967), a density which is

moderate for such forest in New Zealand. The palatability of most tree species was low, but an extensive network of tracks allowed diets to be varied and flowers or fruits to be used irrespective of their distribution. In the Australian habitat described above, social structure and population densities appear to be optimal in relation to food, shelter and ease of movement; but in dense forest (as in New Zealand), with high relative humidity during the winter, heavier populations are required for the maintenance of tracks and an alternative pattern of social structure is found.

There is no evidence of altruistic behaviour, except in relation of mother to young. The marking of tracks by scents, bites or scratches has utility for the community as well as for the marking animal but purposefulness beyond immediate and obvious satisfaction is not apparent. Such lack of conation is indicated by "play" trees. These have bark or outer surface of the type which is generally most preferred for scratching; favourability in this respect seems to compensate for sites which are useless for community purposes. But surface does not induce deposition of scent or urine.

The use of chemical signals or markers (pheromones), derived from special glands, saliva, urine or faeces, is widely recorded and reviewed at least in part by Bourlière (1965). There are many homologies in scent-producing organs or substances among mammals, but diversity of function even among closely related species is such that comparisons become very involved or discriminately subjective and are not attempted here. For the related *Petaurus*, differences rather than likenesses have been considered.

Pheromones carry general information concerning the individual but this varies relatively and seasonally in significance and emphasis. Thomson and Pears (1962) found that secretions of the chest gland and the odiferous pair of the anal glands elicited respective responses that were mild or, with some variation, antagonistic. Accordingly, it would be expected that chest gland imprints would impose little restriction on the use of a track but that anal gland deposits near a shelter would indicate varying probabilities of conflict. Such function of anal glands is unusual in mammals, but *Sminthopsis crassicaudata* (Dasyuridae) is very similar in using anal glands for marking home, not territory (Dr. R. F. Ewer, personal communication).

The slow dripping of urine shows exclusive individual rights, according to the persistence of the marking opossum and the avoidance by others.

This form of marking was induced repeatedly by transfer from the field pens to the town one; and it engendered confidence which was retained for an indefinite period after an opossum had been returned to the field pens. Since detection of the dripped urine trails in forest depends largely on the presence of mosses or small ferns which can retain an imprint of urine visible to an observer, the true incidence is not apparent. Sometimes urine is obviously distributed by a number of opossums but such instances are probably failures of territorial marking, with urine added by successive contestants.

Fighting in captivity was not effective in upsetting territorial claims or in asserting dominance. Only one clear instance was found of fighting for possession of urine-marked poles: a male attacked and defeated a female conclusively during two nights but she continued in her marking and the male returned to his avoidance of the poles. Such fighting, with clearly defined purpose in attack and defence, is unusual. It was not conclusive and physical dominance did not eliminate the effects of scent deposition. Retreat from an attacker, particularly by a female, is not recognised or claimed as admission of inferiority; hierarchical status is accorded little, if any, value.

Fighting, mainly between adult males, is most frequent in autumn — the season of the rut when general activity is greatest. Since under natural circumstances avoidance is always possible during periods of activity, conflict occurs by choice of evenly matched belligerents and so has little effect on competitive exclusion, which is borne by the weaker and retiring members of the community. Among known animals, rivalry has appeared to be personal in that two opossums will fight each other yet ignore similar associates. Such fighting seems to be stimulating for both contestants.

Vocalisation is induced by close proximity but the common *Wuh-uh-uh-uh* is obviously different since it is most frequently made from tree tops. This call seems to be variable in its meaning and communal functions. It is probably phatic, indicating the distribution and movements of vigorous opossums. The clicking sounds suggest uncertainty without anxiety. They have been most frequently noted in exploratory reproductive behaviour of doubtful outcome. All calls, including clicks, seem to be guttural and are modifications of one type of vocalisation. This basic uniformity is not at first apparent, but it would be expected in an early developmental stage of communication.

Ears by their prominence and movement are well suited for semantic functions. They are obvious in mutual contacts of animals and although only few positions are possible, meanings become apparent by situation or associated activity. Modifiers explain the similarity of ear positions in pain and pleasure. Such opposite sensations are clearly separated by other factors.

CONCLUSIONS

The social system of *Trichosurus vulpecula* is based on the individual instead of on pairs or more complex units. Direct visual or acoustic signals between adults are mainly aposematic and indicate risk of conflict rather than threat. Lack of conventionalised dominance and submission prevents group formation, since the response to aggression is fight or escape. Dispersion does not depend on aggression; most usually it results simply from avoidance. Tolerance, in fact, is usually high in respect of weaker animals.

The main communal amenity is a reticulation of tracks on the ground and in trees, which permits efficient utilisation of shelters and foods which have limited availability.

Social marking of prominent objects may be physical as with bites and scratches, or chemical as with pheromones derived from scent glands and urine. In contacts among individuals voice and gesture serve mainly to prevent conflict.

Much behaviour is of ultimate value to both the individual and the community but it appears to be motivated only by a proximate sense of satisfaction.

In habitats which are favourable for low population densities exclusive territories may be established, but an alternative social pattern is effective in dense forest where access tracks can be maintained only by relatively high populations. Territorial space (essentially routes in three dimensions) cannot be defended against many animals and a vigorous opossum may reduce territorial claims to points or short lines which, by their marking, are repellent to other opossums. The holding of territorial stations greatly increases the confidence of captive opossums: in free life it seems probable that, in competing for limited requisites, territorial animals would be unimpeded by the restrictions borne by other members of their community.

ACKNOWLEDGMENTS

I am indebted to Mr. L. T. Pracy for discussion, particularly in the field, and to Mr. W. B. Arnott who was in sole charge of the Orongorongo research station.

REFERENCES

- BATCHELER, C. L., DARWIN, J. H., and PRACY, L. T., 1967. Estimation of opossum (*Trichosurus vulpecula*) population and results of poison trials from trapping data. *N.Z. J. Sci.* 10 (in press).
- BOLLIGER, A., and HARDY, M. H., 1944. The sternal integument of *Trichosurus vulpecula*. *J. Roy. Soc. N.S.W.* 78: 122-33.
- BOLLIGER, A., and WHITTEN, W. K., 1940. Observations on the urine of *Trichosurus vulpecula*. *Aust. J. Sci.* 2: 178.
- BOLLIGER, A., and WHITTEN, W. K., 1948. The para-cloacal (anal) glands of *Trichosurus vulpecula*. *J. Roy. Soc. N.S.W.* 82: 36-43.
- BOURLIERE, F., 1965. *The natural history of mammals*. Knopf, New York.
- BROOM, R., 1898. A contribution to the development of the common phalanger. *Proc. Linn. Soc. N.S.W.* 23: 705-29.
- DUNNET, G. M., 1956. A live-trapping study of the brush-tailed possum *Trichosurus vulpecula* Kerr (Marsupialia). *Wildlife Res. C.S.I.R.O.* 1: 1-18.
- DUNNET, G. M., 1964. A field study of local populations of the brush-tailed possum *Trichosurus vulpecula* in Eastern Australia. *Proc. Zool. Soc. Lond.* 142: 665-95.
- GREEN, L. M. A., 1963. Distribution and comparative histology of cutaneous glands in certain marsupials. *Aust. J. Zool.* 11: 250-72.
- KEAN, R. I., 1967. *Growth and age in Trichosurus vulpecula (Marsupialia)*. Unpublished MS.
- PRACY, L. T., 1962. Introduction and liberation of the opossum (*Trichosurus vulpecula*) into New Zealand. *N.Z. Forest Service Inf. Ser.* No. 45.
- SCHMIDT-NIELSEN, K., 1964. *Desert animals. Physiological problems of heat and water*. Clarendon Press, Oxford.
- SCHULTZE-WESTRUM, T., 1965. Innerartliche Verständigung durch Düfte beim Gleitbeutler. *Zeit. verg. Physiol.* 50: 151-220.
- THOMSON, J. A., and PEARS, F. N., 1962. The functions of the anal glands of the brushtail possum. *Vict. Nat.* 78: 306-8.
- WINTER, J. W., 1963. *Observations on a population of the brush-tailed opossum (Trichosurus vulpecula Kerr)*. M.Sc. Thesis. University of Otago.