https://doi.org/10.26749/rstpp.112.161

Papers and Proceedings of the Royal Society of Tasmania, Volume 112, 1978.

(ms. received 27.8.1977)

OBSERVATIONS ON THE TASMANIAN DEVIL, *SARCOPHILUS HARRISI* (DASYURIDAE: MARSUPIALIA) AT GRANVILLE HARBOUR, 1966-75.

by E.R. Guiler
Department of Zoology, University of Tasmania

(with 15 tables and 14 text-figures)

ABSTRACT

Movements of Tasmanian devils in a western Tasmanian locality, Granville Harbour, were largely restricted to well defined trails and were related to actual or potential food sources.

The sex ratio varied greatly from year to year with the average over 10 years of 1:0.95. The percentage breeding success with females was only 58.9% with 2.67 pouch young/successful breeding female. Recruitment from this source into the adult groups is small.

The population was dominated by large males for most of the period with the recruitment of young, especially of males, being low in most years. Year groups survive in the population for about 5 years. The population is maintained by immigration plus occasional good juvenile recruitment. Young females have a lower mortality than males, possibly resulting from less intraspecific interactions, but the older males have low mortality and live about 1 year longer than females.

The population increased substantially in 1973 due to a high survival of earlier year groups and a low mortality. The Granville devils appear to follow a different population cycle from that of the rest of Tasmania, due to geographic isolation.

INTRODUCTION

Trapping of Tasmanian devils, *Sarcophilus harrisi* (Boitard) at Granville Farm commenced in November, 1966, and is continuing.

In the first period of trapping, between 1965 and 1967, breeding and general features of the population were examined and compared with results obtained from another group of devils at Cape Portland in northeastern Tasmania (Guiler 1970a, 1970b).

The object of this study is to observe the population structure and numbers over a period of years, assess the breeding success and recruitment to the population, and to obtain further knowledge of the movement pattern of devils on the West Coast in an area relatively untouched by agriculture.

Granville Farm was selected because it is remote from any large centre of human population and isolated from human interference, yet much of the area is accessible by 4-wheel drive vehicles so that traps can be carried around the property. A disadvantage is that the area receives so much rain in winter that vehicle work becomes very difficult and, at times, impossible.

METHODS

Devils were trapped using drop-door wire cage traps described earlier (Guiler 1970a) and, after processing the animals were released without removal from their capture site. They were sexed, weighed, measured, young examined and any peculiarities

noted prior to their release. Ear tattoos were used as a method of recognition which, combined with the distribution of the white colour patches on the flanks, chest and rump, enable all the animals to be identified upon recapture.

It was found at Cape Portland that *Sarcophilus* under intensive trapping developed a negative trap consciousness over a period of six months, the yield dropping from 0.337 devils/trap/night to 0.073 (Guiler 1970a). The latter yield returns little information, so it was decided to concentrate on intensive short-term trapping to catch the maximum number of animals for population structure information.

The traps initially were set at randomly selected sites throughout the area of the Farm and the coastal Track leading to Top Farm as well as on the surrounding country. However, based on experience (from 1968) traps were later set along the edges of paddocks, on tracks and on game trails as well as beside dead animals to yield the maximum catch. The trap line was usually about 33km long but whenever traps were set on the Top Farm Track the distance covered was about 53km.

The maximum number of devils usually were caught on the third night of each visit after which, except in 1973 and 1974, the yield declined. It was found that if a trap had not caught an animal in 3 nights at one site it would be most unlikely to do so on future nights so it was shifted to another place. Some sites never yielded a devil and were abandoned.

Throughout this work a visit is the period of a trapping expedition, a year-catch is the animals of mixed ages caught in any one year, and a site is the position of any trap or traps at any one time. A trail is a route used by animals, a track is useable by vehicles.

Granville Farm lies on an isolated part of the West Coast of Tasmania (Lat. 41° 05' E.), the nearest settlement being Granville Harbour about 2 km distant with only 3 permanent residents. The nearest township is Zeehan, 45km away, population 1,200, from which the Farm is accessible only by a rough road. The study area is relatively undisturbed and subject to minimal human interference. A satellite farm, Top Farm, lies 16km to the North and it was unoccupied during most of this study. It is connected to Granville by a coastal track which can be traversed only by 4-wheel drive vehicles and is impassable at times in winter, as well as after heavy rainfalls.

The locality, described by Guiler (1970a), consists of rain forest, gullies, cleared farm paddocks, coastal scrub and dune formations. The edges of all the paddocks have a fringe of *Pteridium* which offers excellent cover for grazing species as well as devils.

Alterations to the fauna list in Guiler (1970a) are the removal of sheep from the property, the absence of *Isoodon obesulus* Shaw and Nodder, the addition of *Ornithorhynchus anatinus* and *Tachyglossus aculeatus*, and an increase in the number of rabbits.

Detailed weather information, other than rainfall, is not available for the Granville area. The area is subject to much wind, mainly from the westerly sector, but there is sufficient shelter in the gullies and scrub for this to have little effect upon the animals living there, other than to force the grazing species to feed close to shelter.

The rainfall (table 1) is moderate but well distributed throughout the year with maximum falls occurring during July/August. The short wet days of winter allow very little drying out of the substratum so that species living there must have a high tolerance for wet and mud. The summer rainfall is highly beneficial giving green

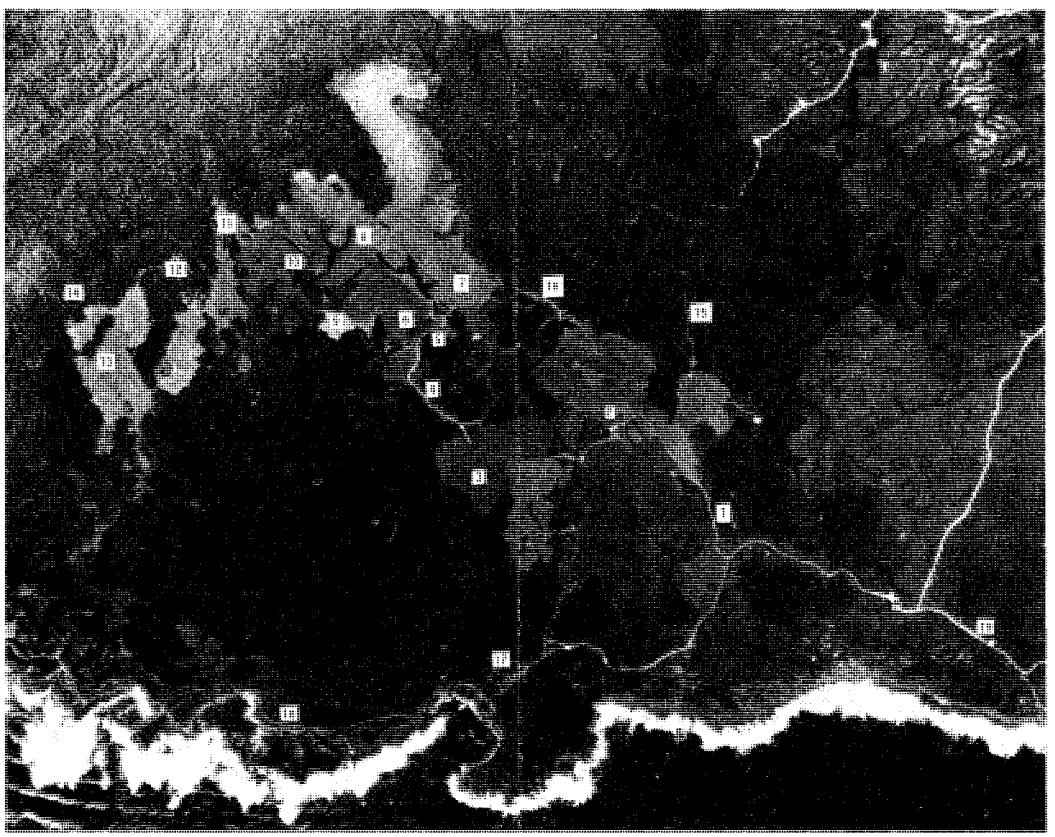


FIG. 1. - Map of Granville Farm area, reproduced by kind permission of the Secretary for Lands. Scale: approx. 1:40,000. Legend: 1. Entrance; 2. Farm; 3. Round Hill; 4. Slaughterhouse Track; 5. Slaughterhouse Track; 6. Harrison's No. 1; 7. Harrison's No. 2; 8. Choumollier Paddock; 9. Five Acre Paddock; 10. Harrison's Back Pockets; 11. Dead Heifer Paddock; 12. Pig Farm; 13. Nicholas'; 14. Duck Creek Track; 15. Zeehan Track; 16. Old Slaughterhouse Track; 17. Granville Town; 18. Track to Top Farm; 19. Tasman River; 20. Stringer's Creek.

TABLE I

RAINFALL (IN MM) RECORDED AT GRANVILLE FARM FOR 1965-74

	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
January	-	78.22	71.37	65.78	89.66	55.12	83.06	90.42	119.63	46.99
February	-	44.70	33.78	97.97	185.93	56.13	86.61	49.02	124.46	64.52
March	-	99.06	77.98	116.33	116.84	25.69	58.17	65.02	148.08	58.17
April	-	162.05	98.80	182.37	159.76	188.47	156.97	158.75	165.61	151.69
May	-	134.37	58.67	307.88	171.96	185.67	188.97	92.20	231.90[x]	24.64
June	-	127.00	98.30	204.72	67.06	147.57	227.84	123.44	177.55	165.86
July	-	270.27	161.04	225.30	211.33	315.21[x]	77.98	239.01[y]	141.99	176.78
August	-	104.90	141.22	225.29	157.23	252.73	253.75	189.74	158.75	99.57
September	-	94.99	134.87	179.83	142.24	151.89	227.84	161.04	126.24	243.33
October	-	132.33	75.18	152.15	62.74	132.59	180.09	56.39	161.29	270.00
November	-	92.71	109.98	186.18	84.07	75.95	113.28	74.42	97.03	81.28
December	-	60.71	118.62	48.75	123.44	118.62	99.57	79.50	114.55	266.70
TOTAL	1477.52	1401.48	1179.84	1992.36	1572.24	1755.6	1754.16	1378.92	1767.0	1644.36

m = 1592.33

All figures recorded above have been recalculated in "mm" from original readings in "inches" and "points" and rounded off.
x - rain on 28 days of the month y - rain on 27 days of the month

pastures throughout the year and providing lush feed for grazers. The daily rainfall is not heavy, the greatest fall being 44.70 mm on 19 August, 1971, but some winter months have rain nearly every day. Snow has never been reported but frosts are common in winter. The microclimate experienced by the fauna can be described as mild with no great or prolonged extremes of temperature. The prolonged winter rainfall could cause discomfort to devils but it also causes stock losses providing food supplies for carrion eaters.

RESULTS

Trapping Details

The trapping details are set out in table 2. In this table, the number of animals caught each visit (Column 3) includes multiple recaptures, the sex ratios being based on this figure, whereas the sex ratio in brackets is based upon the number of unmarked animals caught in each sample.

A total of 282 devils were captured 946 times, 664 of these being recaptures (70.19%). A number of devils were caught on only one occasion (table 3), this percentage ranging from 0 to 39.28 in 1969. Although 50% of the 1975 catch were not retrapped, this percentage can be expected to reduce after subsequent trapping. There was no sex bias in the total number of devils never again trapped though a very strong difference was detected in 1968, 1969, 1971 and 1974. However the adult population showed a strong likelihood that males would be less likely to be recaptured than females whereas the juvenile female was found to be less likely to be recaptured than the male. No such sex difference was detected in either adults or juveniles which were recaptured once during a trapping visit and were not captured subsequently (table 4).

Throughout each visit the number of animals trapped per night declined until it reached such a low level that the return per trap yielded insufficient information commensurate with the effort involved.

TABLE 2

DETAILS OF *SARCOPHILUS* TRAPPING AT GRANVILLE, 1966-74
The figures in brackets refer to new animals only

Date of visit	No. of Traps	Total animals caught	No. of Individuals	No. of new animals	% of new animals	Males	Females	Catch/ Trap/ Night Total	Male	Female
18-23/11/66 10-12/12/66	396	62	40	40	100.0	27(18)	35(22)	0.157	0.068	0.088
30/6-5/7/67	229	46	45	30	66.6	28(16)	18(14)	0.200	0.122	0.078
15-19/11/67	357	19	18	5	27.7	5(1)	14(4)	0.053	0.014	0.039
26/10-1/11/68	331	31	23	15	65.2	10(6)	21(9)	0.093	0.032	0.063
7-11/2/69	367	27	23	12	52.1	12(8)	15(4)	0.074	0.032	0.041
30/5-3/6/69	209	27	17	9	52.9	14(5)	13(4)	0.129	0.067	0.062
16-19/11/69	202	36	17	7	41.1	14(4)	22(3)	0.178	0.069	0.109
3-7/11/70	233	29	20	11	55.0	16(7)	13(4)	0.124	0.068	0.056
30/10-4/11/71	244	37	34	19	55.9	18(6)	20(12)	0.151	0.069	0.082
21-27/11/72	296	45	39	23	58.9	25(13)	20(10)	0.152	0.084	0.067
12-19/5/73	391	106	63	32	50.8	65(18)	41(14)	0.271	0.166	0.104
30/10-3/11/73	335	74	57	23	40.3	42(10)	32(13)	0.221	0.125	0.095
28/5-3/6/74	387	163	99	27	27.2	106(13)	57(14)	0.421	0.273	0.147
2-10/11/74	634	126	71	13	18.3	64(4)	62(9)	0.198	0.100	0.098
25-31/11/75	522	118	69	16	25.5	69(9)	49(7)	0.226	0.132	0.094
	5133	946	635	282			mean =	0.177	0.092	0.082

The catch was lowest in November, 1967, when only 19 animals, a yield of 0.053 animals per trap per night, were captured. Only one of these animals captured was recaptured on this visit although all of the five new animals which were caught were retrapped on later visits. There was no apparent reason for the low catch during this visit, particularly as devils' tracks were numerous throughout the locality.

The catch per trap per night was greatest during 1973 and 1974 reaching 0.421 or almost one animal in every two traps, the mean return over the 1966-75 observations being 0.1766. The increase in 1973 and 1974 may be due to more successful trap siting since 1968 as more was known of the travel routes. However, on each visit the trapping was continued until only retrapped animals were caught so that most of the population were sampled each visit. The return for effort increased from an average of 0.125 in 1966-68 to 0.197 in 1971-73 although the number of traps set declined from 1313 to 1266. This can be interpreted as a sign of a growing population.

The percentage of unmarked devils caught each trip varied around 51.5 from 1967-73 but was lower in 1974.

The yield of new males and females over the period was almost the same, 0.0273 males and 0.0295 females per trap. The total yield of males including retraps, 0.0947, was slightly higher than that of females (0.0815). A substantial sex bias in trapping can be detected in some years, as in November, 1975, November, 1968, and November, 1969. However, in view of the considerable changes in sex ratios observed from year to year it is doubtful if these figures are of any real significance.

A number of animals were caught twice and others were caught on a number of occasions, one male animal, A123, being caught 15 times. Some individual animals were found to show a positive trap consciousness as in the case of a male, A176, which was

TABLE 3

NUMBER OF *SARCOPHILUS* WHICH WERE RECAPTURED ONCE during the year of their original capture and never recaptured subsequently.

	New devils caught	Adults M	Adults F	Juveniles M	Juveniles F	Total	Percentage of Col. 1.
1966	40	6	2	2	5	15	37.5
1967	35	3	1	1	3	8	22.85
1968	15	3	0	0	1	4	26.6
1969	28	7	1	1	2	11	39.28
1970	11	0	0	0	0	0	0
1971	19	1	1	0	2	4	21.05
1972	23	1	0	0	1	2	8.7
1973	55	2	5	3	0	10	18.11
1974	40	0	1	0	4	5	12.5
1975	16	0	0	1	1	2	12.5
		23	11	8	19	61	
		χ^2=4.24		χ^2=4.48			

TABLE 4

NUMBERS OF *SARCOPHILUS* CAUGHT ONLY ONCE. Granville, 1966-75.

	Adults M	Adults F	Juveniles M	Juveniles F	Total
1966	4	3	0	1	8
1967	4	3	1	0	8
1968	0	0	0	1	1
1969	1	1	1	3	6
1970	0	1	0	0	1
1971	0	0	0	0	0
1972	0	1	0	0	1
1973	1	3	3	0	7
1974	4	3	3	7	17
1975	0	0	1	0	1
Totals	14	15	9	12	50
	χ^2=0.03		χ^2=0.43		

caught on six consecutive nights in May, 1973, all in the same locality.

Examination of the trap yield of the different trapping areas (table 5, and Appendix 1) shows that the catch may vary from year to year and also that some areas give much better catches than others. Thus the catch at Round Hill which was high in the early period from 1966-69 declined to such a point that so few devils were caught that it was unprofitable to trap there.

The catching index at certain localities such as the Slaughterhouse is high although the total number of animals caught there is low due to the restricted area in which traps can be set so that a catch of one or two animals per week in one trap leads to a false impression of the number of devils operating in the area.

Round Hill during the period 1965-69 was dominated by female devils by a ratio of 2:1. No other sex differences in trapping were recorded although slightly more males than females were caught on the Zeehan Track.

It was not always possible to trap each area on every visit as weather and track conditions made some places inaccessible, nor was it always possible to set many traps at Granville town as during weekends and holiday periods there was too much interference with traps by dogs and humans.

The table shows that certain areas such as the Dead Heifer Paddock, Pig Farm, Granville Town, Zeehan Track and Nicholas' Paddock yield consistently high catches of devils but these are all surpassed by the 9 acre paddock which has a very high yield from a small number of traps. Most of the animals caught in this paddock were trapped at either a trail under one place in a fence and at a dam across a creek. Trapping the remainder of the paddock has been fruitless, and this experience led to the redesign of the experiment in later years to trap only those stations which yield good catches since it was apparent that devils follow well defined routes and any traps set away from these routes will be of little value.

TABLE 5

CATCHING INDEX FOR *SARCOPHILUS* AT THE MAIN TRAPPING AREAS, GRANVILLE 1965-74. A dash indicates that no traps were set in that locality in that year. The figures are given as catch/1000 traps.

	1965-8	1969	1970	1971	1972	1973	5/1974	11/1974	Mean
Slaughterhouse	50	5	166	-	333	0	-	153	118
Top Farm Track	231	70	-	-	166	102	-	-	142
9 Acre Paddock	250	-	-	333	285	397	764	208	373
Round Hill	153	148	95	67	-	111	-	-	115
Harbour Paddock	48	0	-	41	-	166	-	83	68
Granville	142	333	-	-	-	455	-	250	295
Main Road	42	-	-	166	250	143	-	-	120
Zeehan Track	125	307	-	296	62	363	370	155	240
Harrison's No. 1	133	34	125	-	333	214	150	56	149
Harrison's No. 2	-	-	66	-	-	111	-	159	112
Harrison's Back Pockets	200	173	222	77	28	215	245	139	162
Nicholas' Paddock	153	183	0	-	181	-	552	177	208
Dead Heifer	-	222	350	222	272	230	591	171	294
Pig Farm	-	91	-	-	380	189	574	317	310
Duck Creek Track	100	59	-	0	214	-	230	389	165

Growth of Individuals

Devils are born in April-May and the pouch young can be aged by using various criteria as described by Guiler (1970b). Post-pouch but non-independent devils of up to seven months can be aged by the stage of eruption of the teeth (Guiler and Heddle, 1974). At twelve months of age, during the next breeding season in which they take no part, the young animals weigh about 2½kg. After 12 months of independent life, in November, immature devils weigh about 4.0-5.0kg. The weights of these animals of known age were followed throughout life and used to construct the weight-age relationship curves (fig. 2).

Initially, females are heavier than males but by 18 months this is reversed. There is a large Standard Deviation particularly for males and some individuals showed very great weight increase over a short time so that it is very inaccurate to use weight as an index of age after 18 months. For example, a male, A167, increased in weight from 2.28kg to 7.27kg in six months and a male, A168, from 3.5kg to 9.4kg also in six months. Therefore the age of unmarked devils can only be based upon their external appearance, pelage conditions and the size of the animals and they can only be age-classed as either adult or old animals, the latter being distinguished by lack of postero-dorsal fur, frequently heavy scarring on the face and body, size and sometimes by rheumatism or other neuro-muscular disabilities.

Composition of the population by weight and sex

The mean weight of 100 male devils was 6.91kg, while that of 100 females was 5.39kg. The mean weight of 50 adult males was 8.171kg and that of the same number of females was 6.126kg, and 50 juveniles of each sex showed that the males were slightly heavier, 4.76kg, compared to 4.37kg. Thus, the males are heavier throughout most of the life of the animals, those of 7.75kg or greater usually being males (fig. 3).

The population was arbitrarily divided into six weight groups of which groupings of less than 5.0kg represent immature animals. The weight composition of the population both as a whole and by sexes is considered later (figs. 5-10).

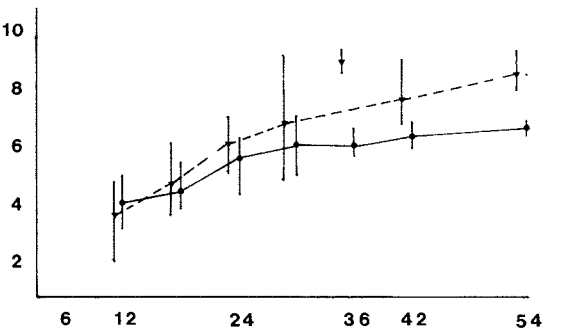


FIG. 2. - Weight (kg; vertical axis)/age (months) relationship for *Sarcophilus harrisi* at Granville. Based on animals of known age. Bars represent the range.

FIG. 3. - Weight distribution (horizontal axis) of 100 each males and female *Sarcophilus* at Granville.

TABLE 6

MEAN WEIGHTS (IN KG) OF BOTH SEXES AND OF THE TOTAL POPULATION (m), EXCLUDING POUCH YOUNG, OF *SARCOPHILUS HARRISI*, GRANVILLE 1966-75.

	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Male	7.77	8.01	8.57	7.82	7.59	8.00	7.51	7.50	7.02	6.80
Female	5.85	6.68	6.44	6.28	6.53	6.33	6.31	5.97	5.92	5.79
m	6.81	7.35	7.51	7.05	7.06	7.17	6.91	6.74	6.47	6.39

The mean weight of the population varies from year to year as also does the weight of each of the sexes (table 6). An unusual situation occurred in 1975 when a number of known survivors from earlier year catches weighing less than 5kg were caught. These would have been classed as immature (weight basis) had they not been known to be of adult age. Furthermore, some of the devils caught in 1975 had reduced body weights compared to those of previous years.

MOVEMENTS

Devils were shown earlier to move up to 16km in a night, although the majority of the population did not travel so great a distance. In addition, it was shown that devils are non-territorial in habit, other than the territory around the immediate vicinity of their food and their mate during breeding (Guiler 1970a). These conclusions have been supported by the results of the present study. Movements of devils were identified in the field by the frequency of usage of trails and by scats and these observations were then confirmed by trapping.

Trapping at Granville revealed that, in general, the devils from the southern end of the property did not move directly up the coast but travelled inland to the eastern paddocks which served as a general mixing area for all of the animals in the district. Similarly devils from the northern parts moved to the east paddocks but not to the southern end of the Farm.

The movement around the Farm is by well defined routes, usually tracks, cattle or game trails. These routes are closely followed by devils and traps placed only one metre distant from the route frequently fail to catch any animals.

MOVEMENTS OF THE SEXES

Some difference was found in the movements of the sexes and, particularly, the Zeehan track area has yielded more information on the movements of females than males. The number of males and females caught and retrapped on the track is approximately the same, but 33% more females than males were retrapped in other localities. The Dead Heifer-Back Pockets-Pig Farm area furnished more male than female retraps.

Males were recaptured a shorter distance from their previous place of capture than females, 170 male recaptures averaging 1.82km from their previous capture station, while 144 female recaptures averaged 2.34km. The greater distance moved by females possibly was the result of greater foraging activity by these animals during the period of maintenance of the young.

SEX RATIO

The sex ratio of the adults, juveniles and pouch young varies considerably from year to year (table 7) as in 1975 when 1.35 adult males were caught for each adult female and in 1971 when seven female juveniles were trapped to three males. The sex ratio varies at different times during one year as in 1967 when the sex ratio of adults in July was found to be 1:0.87 and in November 1:4.0 and also in May, 1973, the sex ratio was 1:0.77 and in November, 1:1.3. These differences may be real or they may be artificial from the small sample sizes. The sex ratio of the whole population excluding pouch young from 1966-75 was 1:1.03 while that of the adults is 1:0.86 and that of the juveniles is 1:1.90 and that of the pouch young is 1:0.94. Chi squared test show that neither the adult nor pouch young ratios differ significantly from 1:1 but the juveniles depart significantly from this ratio. This would suggest a change in the sex ratio from almost equal sexes in the pouch young to a female dominated juvenile population and then a return to a population which, although not significantly different from 1:1 ratio does show a tendency to male dominance in the adults, although the sex ratio of the juvenile and adult populations taken together shows about equal numbers of each sex. The change in sex ratio may be attributed to either a behavioural reaction by the juveniles towards the traps or the sex ratio may be, in fact, different. It is shown earlier that there is no sex bias in the trapping and the juvenile sex ratio may well be a true record of the sex numbers of the population.

TABLE 7

SEX RATIO OF THE GRANVILLE POPULATION OF *SARCOPHILUS HARRISI*, 1966-75.
The total population does not include the pouch young.

	Total Pop.	Adults n.		Juveniles n.		Pouch Young n.	
1966	40	25	15:10 = 1:0.60	15	3:12 = 1:4	20	12:8 = 1:0.67
1967	44	29	14:15 = 1:1.07	15	4:11 = 1:2.75	39	14:25 = 1:1.79
1968	24	20	11:9 = 1:0.82	4	0:4 = 0:4	20	12:8 = 1:0.67
1969	57	45	20:25 = 1:1.25	12	5:7 = 1:1.40	38	11:27 = 1:2.45
1970	21	18	10:8 = 1:0.80	3	1:2 = 1:2.00	20	12:8 = 1:0.67
1971	29	19	11:8 = 1:0.73	10	3:7 = 1:2.33	16	10:6 = 1:0.60
1972	35	28	18:10 = 1:0.56	7	2:5 = 1:2.50	28	16:12 = 1:0.75
1973	94	65	31:34 = 1:1.10	29	17:12 = 1:0.71	43	29:14 = 1:0.48
1974	109	88	49:39 = 1:0.80	21	6:15 = 1:2.50	32	17:15 = 1:0.88
1975	67	61	35:26 = 1:0.74	6	1:5 = 1:5	18	8:10 = 1:1.25
			214:184 = 1:0.86		42:80 = 1:1.90		141:133 = 1:0.94
			χ^2 = 2.26		χ^2 = 11.84		χ^2 = 0.23
			0.20 p 0.10		p .001		070 p 0.50

TABLE 8

CONTINGENCY TABLE ANALYSIS OF INDEPENDENCE BETWEEN SEX-YEARS FOR ADULT *SARCOPHILUS HARRISI* AT GRANVILLE, 1966-75.
The numbers in brackets are the expected values (column total x row total/grand total).

	Males	Females	Total	x^2
1966	15 (13.4)	10 (11.6)	25	0.41
1967	14 (15.6)	15 (13.4)	29	0.35
1968	11 (10.8)	9 (9.2)	20	0.01
1969	20 (24.2)	25 (20.8)	45	1.58
1970	10 (9.7)	8 (8.3)	18	0.02
1971	11 (10.2)	8 (8.8)	19	0.13
1972	18 (15.1)	10 (12.9)	28	1.21
1973	31 (34.9)	34 (30.1)	65	0.95
1974	49 (47.3)	39 (40.7)	88	0.13
1975	35 (32.8)	26 (28.2)	61	0.32
	214	184	398	5.11

χ^2_5 = 5.11;not significant

There was no significant variation in sex ratios for adults over the sampling period (table 8).

REPRODUCTION

Some details of the reproduction of *Sarcophilus* were outlined by Guiler (1970b) who found that the breeding success of *Sarcophilus* varied from year to year. The percentage breeding success at Granville is high with up to 80% of the eligible females carrying pouch young, the mean breeding success of the females being 58.1% (table 9). The years 1967, 1969, 1973, and 1974 were most productive of pouch young though only one of these years (1967) coincided with the highest percentage breeding success amongst the females.

The number of young produced in any year is high relative to the total mature

TABLE 9

REPRODUCTION IN *SARCOPHILUS HARRISI* AT GRANVILLE HARBOUR, 1966-75.
A mature female is one judged to be mature based upon weight and size.

	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	Totals
Total no. of females	22	25	13	28	9	14	14	40	54	31	250
Total mature females	16	16	10	21	6	8	10	29	26	25	167
Females with young	8	12	7	14	4	5	8	18	15	6	97
Females without young	8	4	3	7	2	3	2	11	11	19	70
Percentage success	50	75	70	66.6	66.6	62.5	80	62	57.69	31.5	58.1%
Number of young	20	39	20	38	12	16	16	43	37	18	259
Mean no. of young/female	2.5	3.25	2.85	2.71	3.0	3.20	2.0	2.39	2.46	3.00	2.67

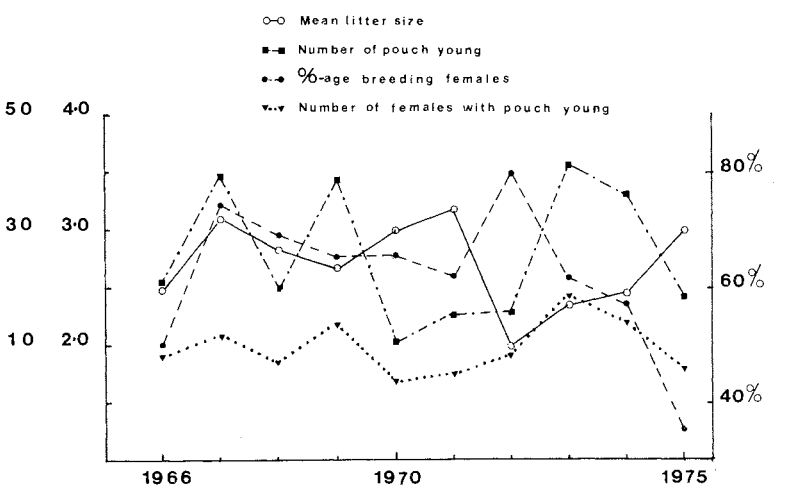


FIG. 4. - Breeding data, *Sarcophilus* at Granville, 1966-75. Outer scale on left side abscissa refers to the number of females with pouch young as well as to the number of pouch young. Inner scale is the mean litter size.

female population in the area. Breeding in 1975 was very unsuccessful with only 31.5% of mature females carrying young although the mean litter size was high (3.0). The number of pouch young is related to the number of breeding females but the percentage breeding success does not follow the number of breeding females in the population (fig. 4).

The mean number of young produced per female and the breeding success each year showed no correlation with rainfall during the months of mating (February-March) or birth (March-April) indicating that breeding in *Sarcophilus* is largely independent of normal weather conditions.

Breeding in the female does not commence until the second breeding season after that in which the female herself was produced, although a few females may carry young in their first year. Some females apparently are never successful in breeding as shown by A692 which was caught each year between 1970 and 1974 inclusive and was not found to be carrying pouch young.

Females breed for about four years and then may still be in the population for a fifth year but not carrying young. Illness may prevent breeding - female A344 had no pouch young in 1967 possibly due to a large cyst on one nipple but the animal bred successfully in 1968 and 1971 when the cyst was not present. In one instance, L. Hughes (pers. comm.) found a uterine cyst in a pseudopregnant female.

A few individuals breed out of phase with the rest of the population as shown by A816, captured on 14/5/1973, having 2 nipples which had been used to suckle large young within about a month, the nipples being much larger than those of the lactating females of the year. Green (1967) reported out of phase young from Icena and Guiler (1970b) found non-synchronous breeders at Cape Portland (N.E. Tasmania).

Young females carrying their first litter have a mean number of 2.0 young and mature animals during their second to fourth seasons have a mean of 3.6 pouch young whereas old animals have 2.0 young in their last season. Assuming a breeding life of five years these figures give a reproductive potential of 14.8 per female which is fairly low. This figure is lower if the mean litter size for all ages (2.67) is calculated with a breeding life of 4 years giving a reproductive potential of 10.68.

LONGEVITY

Devils do not live for a long time in captivity, approximately 6 years being recorded by Flower (1931). However, this would appear to be about the normal life span for an individual as Granville trapping records show that Animal A340, a male, captured on 1/7/1967 as a 3.4kg juvenile of about 12 months age, was last captured on 1/2/74, as an aged, 6.7kg animal. This devil probably was born in March-April of 1966 and was about eight years of age when last captured. Two animals, A325, male, and A344, female, were both estimated on the same criteria to be 6½-7 years of age. The structure of the population weight histograms suggests that males live longer than females and that only a few devils live longer than six years.

EMIGRATION

No evidence could be found of any substantial emigration from the area of Granville-Top Farm. Extralimital trapping at Tasman River, Stringer's Creek and the button grass plains on the Zeehan Track did not produce any marked animals, although a few new individuals were encountered.

PREDATION

Adult *Sarcophilus* do not have any predators in the natural situation, but feral dogs are capable of killing devils. There is both field and experimental evidence that small devils may be deprived of food by large adults, if not actually killed by them (Buchmann and Guiler 1977). No other predators are known, although the small juveniles may well be killed by *Dasyurops maculatus*.

COMPOSITION OF EACH YEAR'S CATCH

The weight-sex composition of each year's catch is described below, together with details of its composition in relation to previous years and the fate of the catch in subsequent years.

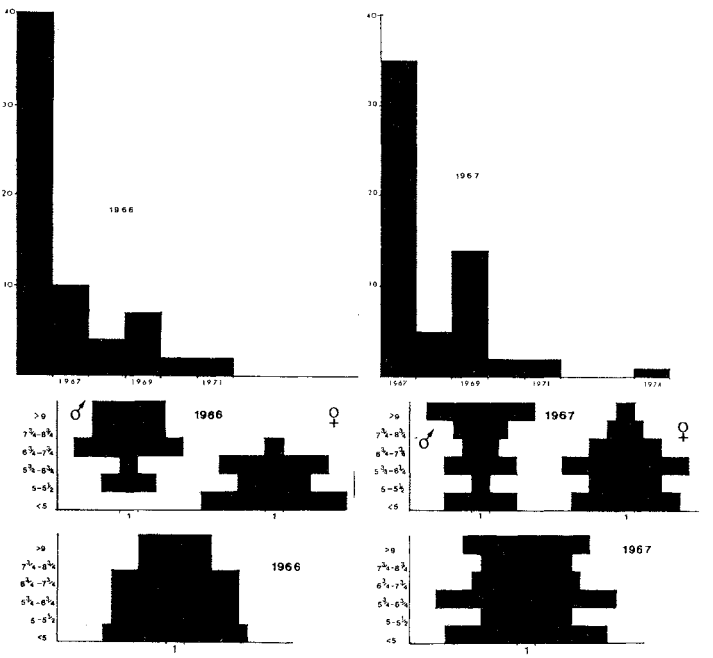


FIG. 5. - Population structure and survival of catch, 1966 and 1967. The lower histogram shows the total population, middle histogram shows the composition by sexes and the top shows the survival of the cohort into subsequent years. The population in this and Figs 6-10 is divided into 6 weight classes (in kg) as shown only on this Figure. In every case in the lower row of histograms males are shown to the left and females to the right of the axis, and in the histograms in the next row upwards males on the left and females on the right histogram.

1966 (fig. 5)

The population showed a good balance between large, medium sized and small animals, but the size distribution in relation to sex showed that all of the small animals of less than 5kg were female. Further, the two largest groups, greater than 7.75kg, were composed exclusively of males. Most of the females of this year were small animals.

The 1966 catch was recaptured in every year until 1971 after which they ceased to appear in the population, but was represented by only one individual in 1970 and 1971.

1967 (fig. 5)

Medium sized devils dominated the population in this year although there were a number of 9kg animals present, one of these being a female, the only animal of that sex to exceed 9kg. The male population in contrast to that of 1966 showed some juvenile recruitment, but again, the largest part of the male group consisted of heavier individuals. The female devils showed good juvenile recruitment with the 5.75 - 6.75kg animals forming the largest group in the population. The large males and

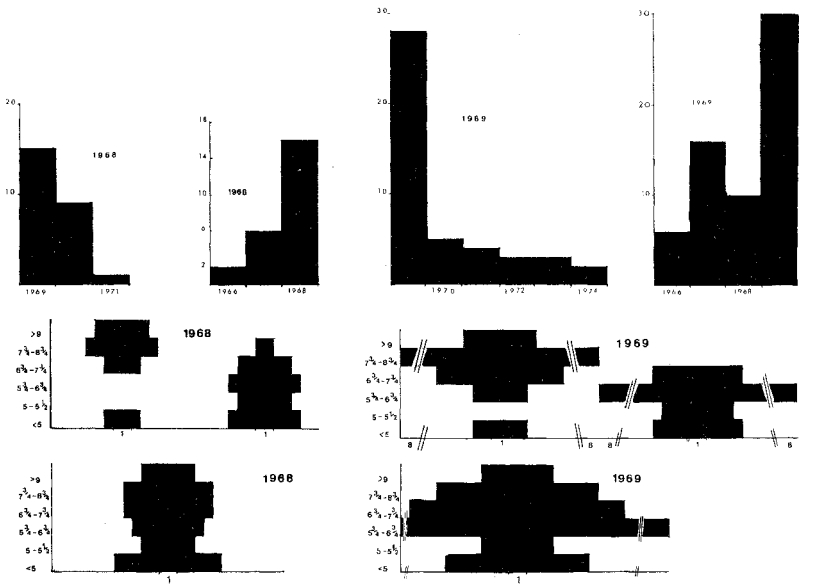


FIG. 6. - Population structure and survival, 1968 and 1969.
Conventions as in Fig. 5.

females formed a very broad summit to the population pyramid.

This catch was very strongly represented in 1969 and although one individual male was recaptured in 1974, most of the animals were no longer seen after 1971.

1968 (fig. 6)

Larger devils again were the most numerous group. However, although recruitment of young apparently was satisfactory, there was a dominance of females in the 5kg group as well as in all groups up to 6.75kg. The male population thus consisted of large animals, a continuation from 1967, together with a very small immature component. The females were of a more balanced composition with good recruitment. The juveniles were composed mainly of females and the next two larger size groups were exclusively female.

The 1968 catch, apart from the new animals of the year, was composed of representatives of the 1966 and 1967 catches and was short-lived, none of the animals being retrapped after 1971.

1969 (fig. 6)

Recruitment of females was greater than that of the males, although the latter showed better recruitment than in 1968, but the number of animals of 5.5kg also was low, probably following the poor recruitment of 1968. Females of 5.75 - 6.75kg formed the largest single group in the population with large males also present in substantial numbers, the heavier male groups forming the largest groups of the population. The population was dominated by large animals of both sexes with young males poorly represented.

This very strong group was identified until 1974 with representation in each year, and contained animals from 1966 with the strongest representation from 1967.

1970 (fig. 7)

Few devils were caught compared to 1969 and the population showed some imbalance with two weight groups poorly represented. Large females greater than 7.75kg were absent and this size group was poorly represented in the males. Some large males were still present, survivors from 1969, forming a substantial part of the male population. Recruitment in both sexes was poor.

These animals survived well and were present in substantial proportions in nearly all years up to and including 1975, although the year 1972 had few members of this group. Representatives from all the previous catches were included in this year.

1971 (fig. 7)

The total population of devils was in a more balanced state although there was considerable imbalance in the male group greater than 9kg, which formed the greatest single group of the male population, and these, together with the next group, formed the largest part of the total population. The young female group was poorly represented, probably resulting from the poor recruitment of the preceding year. Recruitment of males was low, that of the females being satisfactory.

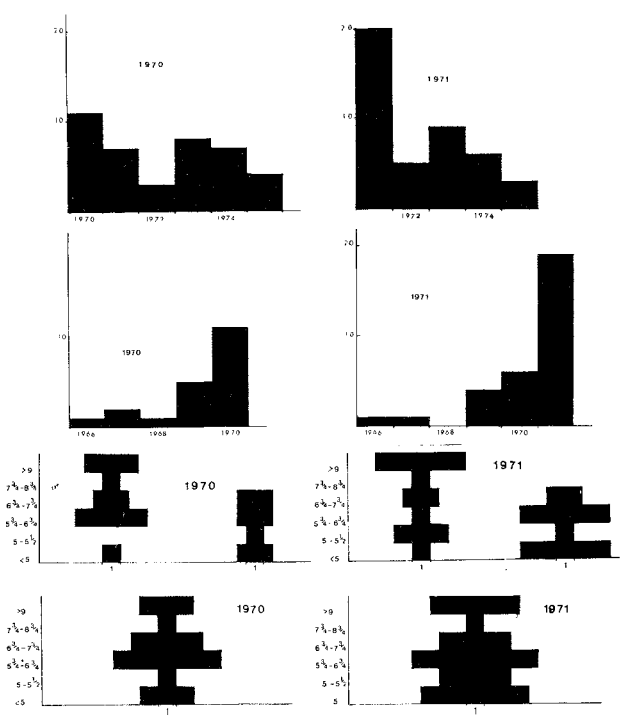


FIG. 7. - Population structure and survival, 1970 and 1971. Conventions as in Fig. 5 adding top right histogram shows the composition of the cohort.

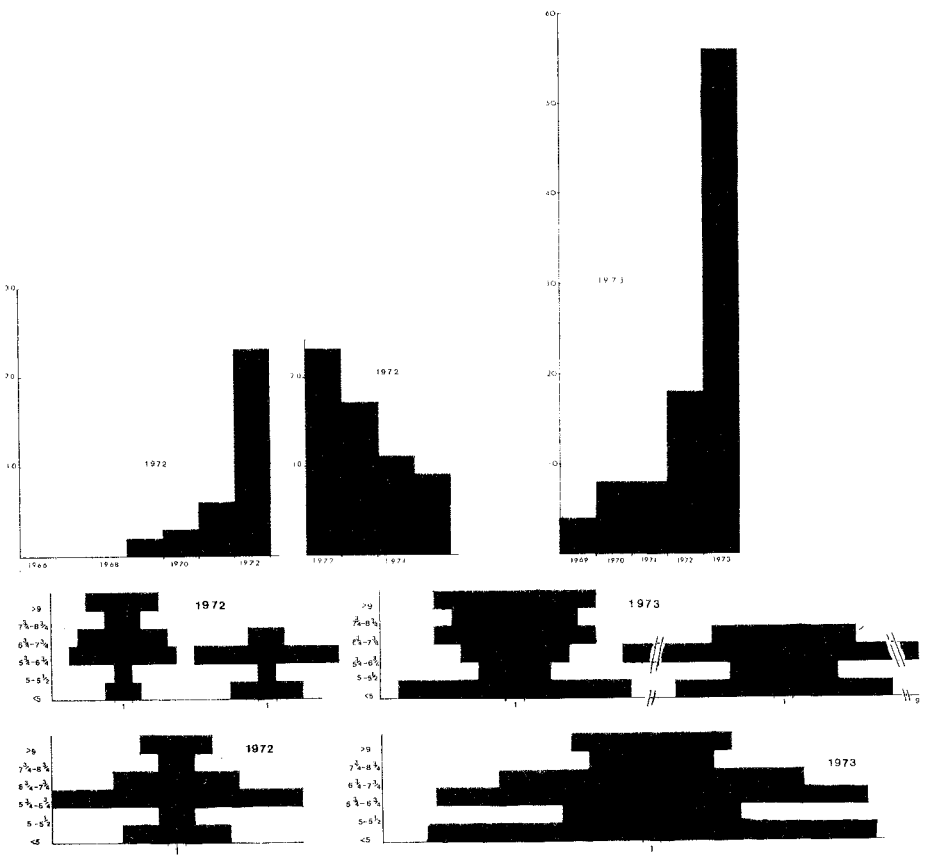


FIG. 8. - Population structure, composition and survival, 1972 and 1973. Conventions as in Fig. 7.

The catch was composed of representatives from all previous years, except those of 1968 which was previously noted as being a short-lived year catch. These devils survived in number until 1975.

1972 (fig. 8)

The number of animals in the Granville area increased this year, mainly because of the appearance of a large number of 5.75 - 6.75kg animals which partially was offset by a low number of young animals. The number of smaller animals was low in both sexes, the two largest size classes being represented only by males. In general both the male and female populations were dominated by medium sized animals. Most of the animals in this year were new to the area and the years 1969-71 were the only earlier groups represented.

This catch was strongly represented in 1973 and again in 1974 showing much better survival than in any other years.

Both the composition of the catch and the weight composition histograms suggest a

large number of new animals in the population, this conclusion being supported by the field records of new captures. As the juvenile recruitment was poor, this was probably due to immigration.

1973 (fig. 8)

The total number of animals increased very substantially due to a general increase in numbers of each weight group rather than to an increase in any particular group or groups. The population showed a good balance between the old, mature, and juvenile weight groups, but the males showed a predominance of large animals, although there was good recruitment of young males. The female production did not have any large animals greater than 7.75kg whereas males of the two heaviest groups formed the largest proportion of the population. Small adult males were poorly represented following on the low recruitment in 1972. Juvenile recruitment was very good in both sexes.

The catch was formed from all groups from 1969. No purpose is served by following the survival of these animals at the present time, although 40 of these animals were caught in 1974 and 19 in 1975.

1974 (fig. 9)

The increase in population found in 1973 continued due largely to a very strong 5.75 - 6.75kg group compsedi almost equally of both sexes. With the exception of this group, the total population showed a very balanced weight group composition. The

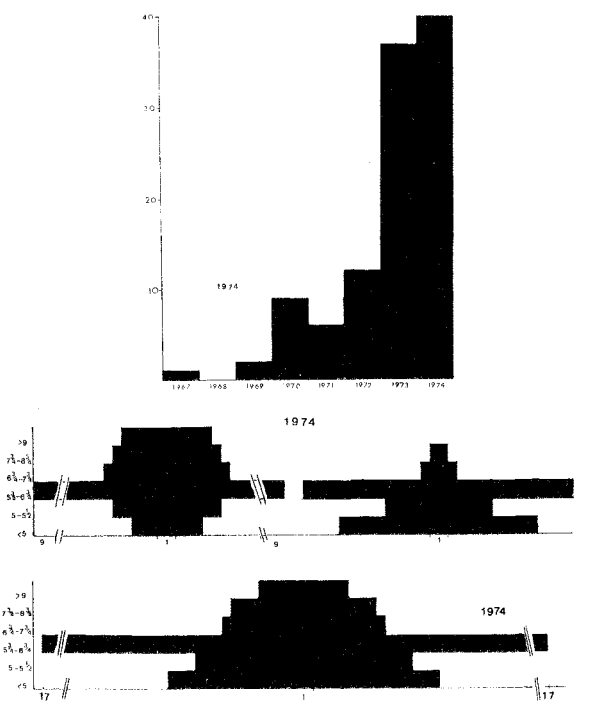


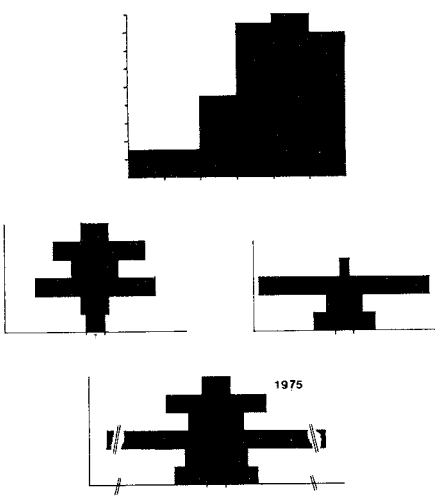
FIG. 9. - Population structure, composition and survival, 1974. Conventions as in Fig. 7.

female population showed good recruitment and a good balance in the larger animals, whereas the males again showed relatively poor recruitment and, apart from the weight groups 5.75 - 6.75kg, a tendency towards "top heaviness" in the population structure.

There was a very strong survival from the 1973 catch, together with representatives of all earlier years except 1966 and 1968; with the 1970 catch being more strongly represented than might be expected. Only eighteen of the 1974 animals were recaptured in 1975.

1975 (fig. 10)

This year's catch was unusual in that the largest number of animals caught were not from the new captures of the year, but from a previous year (1974) and, further, in that the 1973 component also was larger than that of 1975. The survival of the 1973 animals as noted for 1974, continued into 1975, but no animals earlier than 1970 were found although there was a high survival of the 1972 group.



The heavier groups of animals were few in number, especially the females, none of this sex greater than 7.5kg being caught. The very large representation of 5.5 - 6.5kg animals seen in 1974 again occurred, but there was no evidence of the 1974 animals of this size entering the population as larger animals.

The recruitment of both sexes was poor, especially the males, as shown by the small sizes in the 1975 catch.

Although it is not brought out in the figure, this year also was unusual in that the mean weight of each sex was lower than in previous years and, more importantly, some of these low weights of less than 5kg were animals recaptured from previous years and known to be more than 2 years of age.

FIG. 10. - Population structure, composition and survival, 1975. Conventions as in Fig. 7.

ADULT/JUVENILE RATIO

The percentage of adults to juveniles in the Granville population is shown in table 10 to vary from year to year between a very high maximum of 91% and a minimum of 61.53% with a mean of 76.18%, thus emphasising the dominance of adults in the population. In no less than 5 years more than 80% of the population was composed of adults. These percentages are high in comparison with other carnivores. Schaller (1972) found from 40-57% adults in the lions of the Serengeti and Rudnai (1973) recorded about 25% adult lion in Nairobi.

RECRUITMENT

Recruitment to the Granville population is from two sources - immigration or by reproduction. Captured unmarked adult devils may have migrated into the area or may

TABLE 10

PERCENTAGE OF ADULT TO JUVENILE *SARCOPHILUS HARRISI* at Granville Harbour, 1966-75.

	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	Mean %
% Adults	61.53	65.90	83.33	78.94	85.71	65.51	80.00	69.14	80.75	91.04	76.18

have remained unmarked from a previous trip. No immigration estimate could be made for immature animals since these could have been recruited either from breeding within the area or by immigration of young from surrounding areas. All such immatures were considered to be a result of reproductive recruitment whether from within or outside the study area (table 11).

The loss of young devils is very high, ranging from 94.8% to 45.0%, which may be expected from the population structure and mortality curves presented elsewhere. It is evident that in one year, 1972-73, the number of immatures exceeded the number of pouch young by 81%, which indicates a substantial immigration. Apart from this one occurrence, the number of immatures which enter the population is low, indicating a generally low rate of successful reproduction throughout the Farm and its environs.

TABLE 11

RECRUITMENT OF IMMATURE *SARCOPHILUS* FROM THE KNOWN POUCH YOUNG OF THE PREVIOUS YEAR, GRANVILLE, 1966-75.

	1966-67	67-68	68-69	69-70	70-71	71-72	72-73	73-74	74-75	Mean
Pouch young	20	39	20	38	12	16	16	43	37	241
Immatures	10	2	11	2	6	7	29	21	8	96
Loss %	50	94.8	45.0	94.7	50.0	56.3	+81.0	51.2	78.4	60.2

TABLE 12

SURVIVAL OF CATCHES (IN YEARS) OF *SARCOPHILUS HARRISI* AT GRANVILLE, 1969-70.

Year of Capture	Survival (in years)						
	0	1	2	3	4	5	6
1970	11	7	3	8	9	4	0
1969	11	2	1	1	1	0	0
1968	18	8	1	0	0	0	0
1967	30	6	15	3	1	0	0
1966	39	8	2	7	1	1	0

TABLE 13

MORTALITY AND SURVIVAL FOR EACH AGE GROUP OF *SARCOPHILUS HARRISI* AT GRANVILLE. The mortality has been calculated for each age group over the period 1966-74. Expressed as percentages of the survivors of the preceding group.

Age	Total population		Male		Female	
	M	S	M	S	M	S
1.5-2.5	38.8%	61.2%	16.7	83.3	47.8	52.2
2.5-3.5	26.3	73.7	20.0	80.0	40.0	60.0
3.5-4.5	28.6	71.4	33.3	66.6	42.9	57.1
4.5-5.5	40.0	60.0	37.5	62.5	50.0	50.0
5.5-6.5	83.6	16.6	60.0	40.0	100.0	0
6.5-7.5	100.0	0	100.0	0		

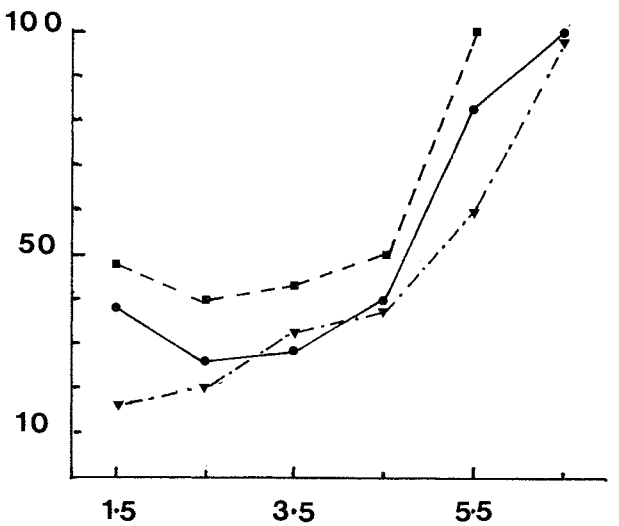


FIG. 11. - Percentage mortality of the age classes of *Sarcophilus*, Granville, 1966-74. Solid line - total population; squares - females; triangles - males. The mortality of the total population is not the mean of that of both sexes because a number of individuals were not sexed at capture.

SURVIVAL AND MORTALITY

The data used in the construction of figs 5-10 were reorganized (tables 12 and 13, fig. 11) to permit the construction of a survivor curve for the populations.

The survival for each group was calculated (table 13). In this table the age groups were calculated from age/weights of known animals and the survival of these groups was derived from marked devils. The curve indicates that there is a heavy early life mortality up to 2.5 years in the female population, and the males suffer a lower mortality rate than the females. The sex ratio changes noted above result from this differential mortality. The female devils disappear from the population before the males.

The low juvenile male mortality rate is unusual in a natural population where the mortality curve usually follows the pattern seen in the female population. This latter type of curve is usually associated with species having a large number of young produced by each female per annum (Seber 1973), a situation which cannot be applied to *Sarcophilus*.

NUMBERS

The population numbers in the area were calculated using four methods - Petersen Index, Modified Petersen Index, Manly-Parr Method (Seber 1973) and Hayne's Graphical Method (Hayne 1949). The estimates so obtained were all close to the observed population at the time (table 14) and no method offered any greater accuracy than another.

In the table, the observed number of devils (1) is the number of individuals caught the preceding November and which are assumed still to be living in the area.

The juvenile recruitment is taken from table 11, mortality was calculated from later records. There is a close correspondence between the calculated population and the observed population and the Petersen Index estimates based upon the trapping results gave very similar population estimates.

The number of devils captured at Granville decreased in 1969 and reached a minimum in 1970 but increased again to reach its maximum in 1974.

The population of devils found in each pair of years was compared for significance (table 15), three pairs of years being found to be highly significantly different at 0.1% level of confidence, namely 1968-1969; 1969-1970; and 1972-1973. Other less significant changes in population numbers were found in 1967-1968 and 1974-1975.

TABLE 14

POPULATION NUMBERS OF *SARCOPHILUS HARRISI* AT GRANVILLE, 1967-75.

Year	Observed Population (1)	Juvenile Recruitment	Immigration	Mortality	Calculated Population	Observed Population (2)	Petersen Index
1967	40	10	7	11	46	45	64
1968	45	2	7	6	48	23	21
1969	23	11	16	9	41	59	63
1970	59	2	11	58	14	20	20
1971	20	6	19	11	34	34	35
1972	34	7	17	22	36	39	46
1973	39	29	36	17	87	92	77
1974	92	21	21	45	89	106	100
1975	106	8	8	15	107	69	138

The Observed Population (1) is that found in November of the previous year; juvenile recruitment is the number of pouch young of the preceding year plus immigrant young (if any); immigration is the number of unmarked adults found in the area; mortality - animals never again trapped; calculated population is the sum of Columns 1-4; Observed Population (2) is the number of individuals caught in that year.

BIOMASS

The biomass of devils at Granville was calculated for each year (fig. 13). An increase in the number of devils corresponded to an equivalent increase in biomass except in 1971 when the biomass increase was less than might be expected and this may be attributed to the small number of devils of less than 7kg in the population (fig. 7).

The nutritional requirements of *Sarcophilus* are not known but assuming that the nutritional requirements of a dog of 6.8kg to be equivalent to that of a devil of the same weight, its requirements would be 0.43kg wet wt. of meat/day (following the Nutritional Research Council recommendations (1974)). Two Hereford cows die each month on the property and are left to the devils and assuming each beast to weight 500 kg of

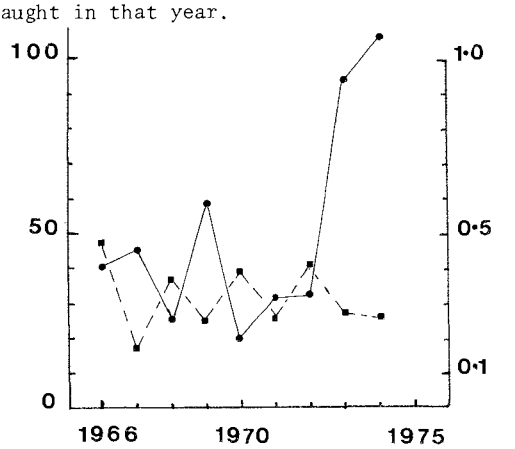


FIG. 12. - Numbers of *Sarcophilus* population at Granville in relation to the mortality, 1966-74.

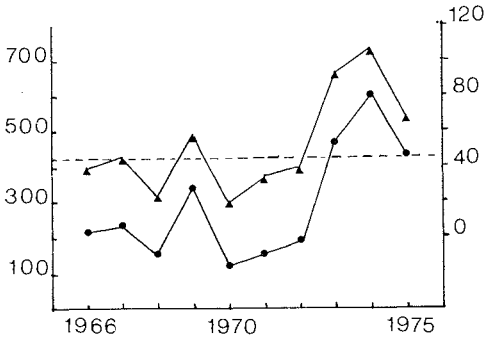


FIG. 13. - Biomass and numbers of *Sarcophilus* at Granville, 1966-75. Triangles indicate the numbers. Biomass (abscissa) in kilograms. Dotted line is the annual sustainable biomass of devils which can be maintained by cattle losses.

which 12% is bone and 40kg is digesta, the weight of available material is 400kg. Thus 24 Herefords/annum will support 415.92kg of devils/annum.

The population of devils in seven of the ten study years was at or below this level (fig. 13) so that it can be concluded that the population can be sustained at about 44 animals feeding on cattle losses alone, apart from other food sources such as carcases from game control operations, natural deaths of wild species and other foods. The use of food sources from agricultural activities can sustain a *Sarcophilus* population at Granville without total dependence on natural food resources or, alternatively, can maintain a population above that which would be sustained by normal food resources.

TABLE 15

CHI-SQUARE ANALYSIS OF PAIRED YEARS OF THE POPULATION OF *SARCOPHILUS HARRISI* AT GRANVILLE HARBOUR, 1966-75.

	Observed Population	Expected Population	χ^2	Significance
1966	40			
		42.5	0.29	N.S.
1967	45			
		34	7.12	++
1968	23			
		41	15.8	+++
1969	59			
		39.5	22.7	+++
1970	20			
		27	3.63	N.S.
1971	34			
		36.5	0.34	N.S.
1972	39			
		65.5	21.44	+++
1973	92			
		99	0.99	N.S.
1974	106			
		87.5	7.82	++
1975	69			

It is assumed that the expected population is the mean of each pair. N.S. - not significant; ++ - significant at 1% level of confidence; +++ - significant at 0.1% level of confidence.

DISCUSSION

The movements of devils around the property were found to be confined to several well defined trails with certain parts of the Farm being more heavily used than others. Adventitious food sources such as dead cattle serve as temporary attractions in any

region, but nevertheless certain overall activity patterns could be identified.

The decline in the number of captures on Round Hill in 1970 was most remarkable, only three of the trap sites yielding any animals during that year. Nevertheless the catching index for the Farms was approximately the same as usual, indicating that the devils were still in the general area and the field records showed that the emphasis of activity had shifted to the Dead Heifer Paddock-Pig Farm area. Sheep used to be kept on the Round Hill and were gradually removed in 1969-71. It has been found from experience elsewhere, that devils collect around sheep paddocks presumably attracted by the likelihood of obtaining food from dead or cast sheep and the withdrawal of sheep from Round Hill may well be the cause of the decline in devil numbers in that area.

The movement of devils to the Dead Heifer Pig-Farm area probably is also associated with the availability of food since numbers of *Wallabia* and *Thylogale* are shot around the edges of these paddocks as a game control operation, and this area is central to other paddocks in which shooting takes place. Also, the area is on the direct route via Duck Creek to Top Farm.

The distribution of devils on the Farm probably is related to potential and actual sources of food and the trails used by them are the most direct routes between these places. Devils favour cover whenever possible and move along certain well defined trails, traps set on these tracks nearly always make good catches although adjoining sites rarely make a capture.

It is clear that there often is a very considerable annual change in the population structure, this change usually appearing in animals other than immatures, namely other than by recruitment of pouch young. These animals may be expected to come from two possible sources, namely by immigration of new animals from the surrounding country or by a return of previously marked animals into the study area. The latter occurred in 1973 and 1974 when a high proportion of the 1970 cohort were retrapped after not having been caught in 1971 and 1972. The Farm offers attractive habitat for devils due to the ready availability of food from the game control operations as well as from deaths of agricultural stock so that animals will tend to remain in the area once they have entered it and emigration is unusual.

The survival of each catch follows a common pattern, a high percentage of each year's catch disappearing during the year subsequent to initial capture. This pattern was not followed by the 1970 cohort as the majority of this group were recaptured in 1973 and 1974, with strong survival in 1975.

The composition of each year's catch also follows similar patterns, most of the animals being new animals of the year, either by juvenile recruitments or by immigration. However, 1974 was unusual in that there were a large number of 1973 survivors in that cohort. Although there was a high percentage of 1970 survivors, these comprised only a small number of the large total catch.

The population in 1975 showed very unusual features in that there were a number of animals caught as juveniles in 1974, weight 5 4 kg, were recaptured when their weight fell into the same size class. These animals were adult by that time but this was not shown by a weight gain. Further, some adults of 1974 or earlier, were recaptured weighing less than in 1975. It can be speculated that food shortage led to this situation, but there was no field evidence that this was in fact so.

The annual population weight structure varies considerably from year to year, but generally shows dominance by one of the adult size groups, except in 1966 and 1973 when immatures formed the largest group. Recruitment into the population from pouch young was low in all years except in 1973 and 1974. This is especially true of the

males when 1973 was the only year in which there was a large male recruitment from pouch young. This would perhaps suggest that the male population is largely maintained by a low annual rate reinforced by sporadic good recruitment.

The largest size group, 9kg, was, with the exception of 1967 when one female reached that weight, entirely composed of males. The largest proportion of the male population was composed of animals of greater than 7.75kg, although exceptions occurred in 1973 and 1974. These large males were always more numerous than females of the same weight groups. It has been shown (Buchmann and Guiler 1977), that social dominance is largely controlled by the size of the individual devil, so it follows that there are considerable behavioural and social implications in the dominance of the population by large males. Intraspecific competition occurs around food, and in the natural situation at Granville the food is concentrated into restricted sites around carcases so that the larger and aggressive males will be able to deny or restrict access by other devils. Recruitment of juvenile males into the population is usually low, 1973 being the only exception. The sex ratio of pouch young is 1:0.95 and that of juveniles is 1:1.67 suggesting a differential mortality between these two age groups and this may well be due to the social and numerical dominance of large males having a greater effect upon male than female recruitment.

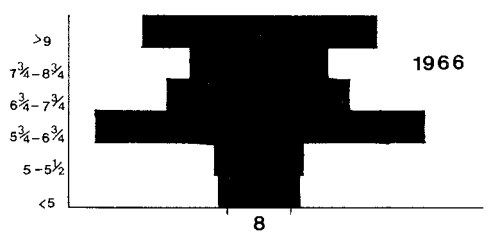


FIG. 14. - Population structure for *Sarcophilus harrisi* at Cape Portland, north-eastern Tasmania, 1966.

Dominance of the population by large males is not confined to the Granville area as Cape Portland showed the same composition in 1966 (fig. 14). However, in a population at Auburn where annual cropping takes place as a control measure, there are only small numbers of large males and juvenile recruitment is correspondingly high, annual samples showing a high proportion of males of 5.75kg.

The recruitment from pouch young is low with losses up to 94.7% being recorded, but in 1972-73 the recruitment was 81% greater than the numbers of pouch young recorded in the area. This probably resulted from an immigration of young juveniles into the area following successful breeding in the adjoining country.

The mortality curves shows a differential mortality rate between the sexes, females having a higher mortality in the 1.5-2.5 year animals, whereas the males have a lower rate than the females throughout life. The sex ratio of the population shows the effects of this differential mortality, the sex ratio of the pouch young slightly favouring males, whereas the females dominate the young stages followed by a strong dominance by the males in the adults. It has been suggested above that the poor male recruitment is a result of social interactions at feeding sites leading to a female dominance of the 0.5-1.5 year group. Any uniform mortality upon this group must cause higher female death rates.

It has been shown that *Sarcophilus* does not gain most of its food by predation (Buchmann and Guiler, 1976, and in preparation) and most of its food is obtained from carrion. Comparative data for eutherian species of similar habitats are not available although Kruuk (1972) showed that mortality in the spotted hyaena in Ngorongoro is high (1.8) up to 3 years and then low for a further 3 years and then remaining at 1.0 for the rest of life. However, he found that recruitment was much greater than in the devil. Similar mortality was found in the black bear where 13% die between 0.5 and 1.5 years which is low but this is followed by high mortality (Jonkel and McCowan 1971). By contrast the mortality in *Sarcophilus* at Granville is very high in the 0-1.5 year

groups and recruitment is based largely upon immigration from the surrounding areas, probably on account of the attractiveness of the Farm rather than to any major surplus of animals in the surrounding country.

The population at Granville from 1966-70 differed significantly from year to year, then the number of animals increased sharply and highly significantly in 1973 and this population level was maintained in 1974 due largely to high immigration but assisted by a high survival of earlier year catches combined with a low mortality rate. No apparent reason can be found for this increase, the amount of food being no greater than that of previous years nor was there less predation upon the devils. The number of devils at Granville in 1975 was significantly less than those in the previous year. The field evidence such as footprints, and scats, supported this, but there was ample similar evidence that numbers of devils were at Top Farm, attracted there by an intense game control shooting programme. These animals may be caught in a later year.

The Granville area in 1966 at the start of this work had small numbers of devils in comparison with other parts of Tasmania (Guiler 1970a), and the population throughout Tasmania has increased steadily since 1958 so that they now are numerous in many places where they were unknown 20 years ago. One of the features of this population explosion was the short time in which it occurred, taking about five years to spread over the State. There is no evidence in this field study of any contemporaneous increase in numbers at Granville, rather to the contrary in 1968, 1970-72, and it was not until 1973 that the population expanded rapidly. Many other pastoral properties in Tasmania still have many more devils than are found at Granville, e.g. Auburn where 250 were taken in one year (1974) as a control measure. From this, it would seem as if the Granville population has been slow to react to the factor or factors causing the population explosion over much of the rest of Tasmania. On the other hand, the Granville devils may form a separate population from those in the other parts of the State.

The Granville devils are smaller and weigh less than those at Cape Portland, but this does not necessarily establish a geographical race or separate population, being more likely to be a result of the nutritional status of the individuals, those at Cape Portland living on mixed sheep-cattle pastoral area and being very much better fed than the Granville animals. Examination of a series of skulls from each area failed to reveal any major differences to suggest separate races. Nevertheless, the Granville animals are geographically isolated from those living in the farming area of the State, the Pieman River to the North and Macquarie Harbour to the South and the rainforests to the East forming boundaries through which little if any exchange of animals can take place. With the exception of Granville and Top Farm, there is no agriculture in all of the Pieman-Macquarie Harbour area so that food availability in the area has not altered due to increased farming since 1976. Rather to the contrary as sheep farming has ceased in the area during this study. The ability of cattle losses to support a devil population without recourse to natural food emphasises the fact that *Sarcophilus* has profited from white man's presence in Tasmania.

ACKNOWLEDGEMENTS

I am indebted to Mr. G. Smith of Granville, not only for his permission to trap on his property, but also for accommodation and traditional hospitality while there. Messrs. D. Smith and J. Reynolds have helped us in many ways during our trapping trips and we are very grateful to them. Mr. T. Sward of this Department has been my faithful field assistant without whose efforts the whole project would be less complete.

The project was supported by a University of Tasmania Research Grant and permission to trap devils was kindly granted by the Director, National Parks and Wildlife Service. I am grateful to the staff of the latter Department for samples of devils which they collected.

Professor G.B. Sharman very kindly commented upon a draft of this paper.

REFERENCES

Buchmann, O.L.K. and Guiler, E.R., 1977: Recent behavioural and ecological studies on the Tasmanian devil, *Sarcophilus harrisii* (Boitard) (Dasyuridae:Marsupialia). BIOLOGY OF MARSUPIALS, MacMillan, London, 155-68.

Caughley, G., 1967: Calculation of population mortality rate and life expectancy for thar and kangaroos from the ratio of juveniles to adults. *N.Z. J. Sci.*, 10, 578-84.

Flower, S.S., 1931: Contributions to our knowledge of the duration of life in vertebrate animals. *Proc. Zool. Soc. Lond.*, 1931, 145-234.

Green, R.H., 1967: Notes of the devil *(Sarcophilus harrisii)* and the quoll *(Dasyurus viverrinus)* in north-eastern Tasmania. *Rec. Queen Vict. Mus.*, 27, 1-12.

Guiler, E.R., 1970a: Observations on the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia:Dasyuridae). I. Numbers, home range, movements and food in two populations. *Aust. J. Zool.*, 18, 49-62.

_____, 1970b: Observations on the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia:Dasyuridae). II. Reproduction, breeding and growth of pouch young. *Aust. J. Zool.*, 18, 63-70.

_____, 1970c: The Tasmanian devil and agriculture. *Tasm. J. Agric.*, 42, 134-7.

_____ and Heddle, R.W.L., 1974: The eruption and growth of teeth in the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia:Dasyuridae). *Pap. Proc. R. Soc. Tasm.*, 108, 137-40.

Hayne, D.W., 1949: Two methods for estimating populations of mammals from trapping records. *J. Mammal.*, 30, 399-411.

Jonkel, C.J. and McCowan, I. McT., 1971: The Black Bear in the Spruce-Fir forest. *Wildl. Monogr.*, 27, 1-57.

Kruuk, H., 1972: THE SPOTTED HYAENA, Chicago Univ. Press, Chicago.

Rudnai, J.A., 1973: SOCIAL BEHAVIOUR OF THE LION, Golden Press, New York.

Schaller, G.E., 1972: THE SERENGETI LION, Chicago Univ. Press, Chicago.

Seber, G.A.F., 1973: THE ESTIMATION OF ANIMAL ABUNDANCE AND RELATED PARAMETERS, Griffin, London.

APPENDIX 1.

Numbers of *Sarcophilus* by sex captured at Granville 1965-74, together with the number of traps and the calculated catch/1000 traps.

	1965-8					1969					1970					1971				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Slaughterhouse	11	7	8	159	50	0	1	1	5	200	0	1	1	6	166	0	0	0	0	0
Top Farm	5	7	12	63	190	0	0	0	0	-										
Top Farm Track	12	10	22	95	231	3	4	7	99	70										
Acre	1	2	3	12	250	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Round Hill	27	30	57	372	153	18	13	31	209	148	6	4	10	105	95	5	1	6	18	333
Fairfields	5	10	15	198	75	1	2	3	43	69	1	1	2	35	57	1	2	3	45	67
Harbour Paddock	0	1	1	21	48	0	0	0	9	0	0	0	0	0	0	0	2	2	14	142
Main Road	1	3	4	94	42	0	0	0	5	0	0	0	0	0	0	0	1	1	24	41
Barn	4	1	5	44	113	0	0	0	0	0	0	0	0	0	0	2	0	2	12	166
Harrison's No.1	5	5	10	75	133	1	3	4	118	34	1	1	2	16	125	0	0	0	0	0
Harrison's No.2	0	0	0	8	0	0	0	0	0	0	1	0	1	15	66	0	0	0	0	0
Nicholas' Paddock	1	1	2	13	153	6	5	11	60	183	0	0	0	9	0	0	0	0	0	0
Harrison's Back Pockets	0	1	1	5	200	4	9	13	75	173	4	2	6	27	222	1	1	2	26	77
Duck Creek Track	0	1	1	10	100	2	4	6	101	59	0	0	0	0	0	0	0	0	12	
The Farm	4	2	6	54	111	0	2	2	6	333	0	0	0	0	0	0	0	0	12	0
Granville Town	2	0	2	14	142	1	1	2	6	332	0	0	0	0	0	0	0	0	0	0
Zeehan Track	0	5	5	40	125	2	2	4	13	307	0	0	0	0	0	6	10	16	54	296
Dead Heifer	0	0	0	0	0	2	2	4	18	222	3	4	7	20	350	3	3	6	27	222
Pig Farm	0	0	0	0	0	0	2	2	11	91	0	0	0	0	0	0	0	0	0	0

A = number of males; B = number of females; C = Total; D = number of traps; E = catch/1000 traps.

APPENDIX 1 (continued)

Numbers of *Sarcophilus* by sex captured at Granville 1965-74, together with the number of traps and the calculated catch/1000 traps.

	1972					1973					May 1974					Nov. 1974				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Slaughterhouse	0	1	1	3	333	0	0	0	6	0	0	0	0	0	0	2	1	3	13	153
Top Farm																0	0	0	0	0
Top Farm Track						3	2	5	49	102	0	0	0	0	0	0	0	0	0	0
Acre	1	0	1	6	166	6	5	11	29	379	11	2	13	17	764	4	1	5	24	208
Round Hill	1	0	1	6	285	1	1	2	18	111	0	0	0	0	0	0	0	0	0	0
Fairfields	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harbour Paddock	0	0	0	0	0	1	0	1	6	166	0	0	0	0	0	1	0	1	12	83
Main Road	0	0	0	0	0	10	1	11	77	143	0	0	0	0	0	0	0	0	0	0
Barn	0	1	1	4	250											0	0	0	0	0
Harrison's No.1	0	1	1	3	333	4	2	6	28	214	2	1	3	20	150	1	0	1	18	56
Harrison's No.2	0	0	0	0	0	2	2	4	36	111	0	0	0	0	0	3	4	7	44	159
Nicholas' Paddock	6	2	8	44	181	0	0	0	0	0	16	7	23	44	552	3	5	8	45	177
Harrison's Back Pockets	1	0	1	35	28	9	5	14	65	215	9	6	15	61	245	4	6	10	72	139
Duck Creek Track	3	3	6	20	214	0	0	0	0	0	3	3	6	26	230	2	12	14	36	389
The Farm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Granville Town	0	0	0	0	0	7	13	20	44	455	0	0	0	0	0	2	2	4	16	250
Zeehan Track	3	4	7	112	62	44	24	68	187	363	28	15	43	116	370	16	10	26	168	155
Dead Heifer	5	4	9	33	272	12	9	21	91	230	20	9	29	49	591	6	8	14	82	171
Pig Farm	5	3	8	21	380	8	9	17	90	189	17	14	31	54	574	20	13	33	104	317

A = number of males; B = number of females; C = Total; D = number of traps; E = catch/1000 traps.