Time budgets and activity patterns of sub-Antarctic fur seals at Gough Island

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The diurnal activity patterns of sub-Antarctic fur seals, *Arctocephalus tropicalis*, were observed at a non-breeding colony site at Gough Island (40°20'S, 9°54'W) during summer. Time budgets of adult males were also studied at idle and breeding colony sites. Levels of activity were highest during the early morning and late afternoon. High ambient temperatures depressed the interaction rate on the dry hauling ground, but activity increased as a result of the movement of heat-stressed seals to and from the sea where favourable conditions for heat loss exist. The fur seals were largely inactive, in particular adult males which spent 93,2% of the time inactive in breeding colonies and 97,9% of the time inactive at idle colony beaches. The daily change in numbers ashore, the relative contribution of the different age and sex classes, their location and distribution on site, and the prevailing weather conditions influence the pattern of interaction and allocation of time to the various activities in *A. tropicalis*. The predominance of inactivity is considered to be a behavioural thermoregulatory response to limit endogenous heat production as is energy conservation. Both views translate into improved tenure for territorial males, in particular those without access to water for cooling during the breeding season.

Die aktiwiteitspatrone van sub-Antarktiese pelsrobbe, *Arctocephalus tropicalis*, is gedurende die dag by 'n nie-teelkolonie te Gougheiland gedurende die somer waargeneem. Tydsbegrotings van volwasse mannetjies is ook by vrygesel- en teelkolonies bestudeer. Vlakke van aktiwiteit was die hoogste gedurende die vroeë oggend en laat namiddag. Hoë omgewingstemperature het die tempo van interaksie op die droë strandgebied versnel, maar aktiwiteit het toegeneem as gevolg van die beweging van robbe wat deur die hitte affekteer is, na en van die see waar voordelige omstandighede vir hitteverlies heers. Die pelsrobbe was hoofsaaklik onaktief, in besonder volwasse mannetjies, wat 93,2% van hul tyd in teelkolonies en tot 97,9% van die tyd onaktief in vrygesel kolonies verkeer het. Die daaglikse verandering in getalle aan wal, die relatiewe bydrae van die verskillende ouderdom- en geslagsklasse, hul posisie en verspreiding op die strand, en die heersende weersomstandighede beïnvloed die patroon van interaksie en toedeling van tyd aan die verskeie aktiwiteite in *A. tropicalis*. Die oorheersende onaktiwiteit word beskou as hittereguleringsgedrag om endogene hitteproduksie te beperk soos met energiebesparing. Beide gesigspunte vertolk in verbeterde eiendomsreg, in besonder vir territoriale mannetjies sonder toegang tot water vir afkoeling gedurende die somer.

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In pinnipeds, at least one sex undergoes a prolonged fast during the breeding season, relying on blubber reserves for energy, and it has been hypothesized that the low level of activity is determined by finite energy resources (Stirling 1971; Harwood 1976; Sandgren 1976; McCann 1983; Anderson & Harwood 1985). In otariids, this seems to be particularly evident in males and Stirling (1971) attributed their relatively low activity to conserving energy which would prolong their presence at the breeding colony and increase their reproductive potential (the 'energy conservation' hypothesis).

On the other hand, otariids, with their heat-retaining pelage and layer of subcutaneous blubber of varying thickness, which restricts heat loss to water because of its high thermal capacity, are adapted to conserve heat in their normally cold marine surroundings. They are unable to regulate their body temperature effectively on land by physiological means alone during thermal loading (Whittow, Matsuura & Ohata 1975). Behavioural means are required to supplement physiological thermoregulation. This includes flipper waving, postural adjustments, use of shade, urohidrosis, panting and open-mouthed type of breathing or resorting to water and/or wet sand (Bartholomew & Wilke 1956; Orr 1967; Rand 1967; Stirling 1970; Gentry 1973; Odell 1974; Miller 1974; Vaz-Ferreira 1975; Whittow *et al.* 1975). Behavioural thermoregulation may therefore substantially influence the activity patterns of fur seals when they are ashore, and their relatively low level of activity might be a behavioural response to restrict endogenous heat-loading (the 'thermoregulatory' hypothesis).

The original study into the activity of *A. tropicalis* at mid-latitude Gough Island was done to increase our knowledge of the then poorly known fur seal species (Bester 1977). The particular local distribution pattern and habitat selection of the different colony types of fur seals during the summer breeding (pupping and mating) season was ascribed to a behavioural response to reduce exogenous heat-loading (Bester 1982a). The present study attempts to test the 'thermoregulatory' and 'energy conservation' hypotheses for the on site behaviour of the species by investigating the time budgets and diurnal activity patterns of:

1. Fur seals in non-breeding colonies, where territory maintenance and breeding are rare and 'thermoregulatory' concerns presumably take precedence over 'energy conservation'.
2. Adult males in different social settings, where the behaviour of territorial males in breeding colonies with access to females is presumably commensurate with 'energy

conservation', while those adult males largely without territories and females in non-breeding colonies, or without territories and females in idle colonies, are expected to be 'thermoregulatory' orientated.

Methods

Observations on *A. tropicalis* were made on Gough Island (40°20'S, 9°54'W) during daylight hours in the austral summers of 1974/75 and 1975/76. The time devoted to different behaviour patterns was estimated from high vantage points at the back of idle, non-breeding and breeding colony sites (defined by Bester 1982a) using scan sampling at intervals of 5–15 min appropriate to the number of animals present (Altmann 1974). The time lapse between scans was constant for each observation period. Observations were usually spread over the period 08:00 – 16:00 and incorporated a wide range of ambient temperatures. Most observations were made on east-facing idle (Admiral Beach north), non-breeding (Seal Beach), and breeding (South Point Beach) colony sites which were 24–30 m wide and backed by 30–200-m perpendicular cliffs which sheltered them from the prevailing westerly winds (Bester 1977). Ancillary observations were made at an idle and a breeding colony beach in Snug Harbour on the south coast. Effort was concentrated on the Seal Beach non-breeding colony site which sloped gently towards the inshore area which had a shallow bottom gradient and a relatively wide surf (wet) zone which shifted with the tides. Direct solar radiation, modified by cloud cover and shade (which advanced progressively across the beach from local apparent noon) and ambient temperature, but not wind, were the conspicuous factors operational at these east coast sites. Ambient air temperatures were measured at the observation point, with a shaded mercury bulb thermometer, at the conclusion of each scan. This provided a measure of diurnal temperature trend, not of actual ambient temperature and influence of direct solar radiation experienced by the seals on the site. The threshold value of 18,5°C determined here is defined as the air temperature value at which the fur seal males on the dry hauling ground started abandoning the spread flipper posture (Stirling 1970; 1971; Gentry 1973; Bester 1977) in favour of movement to the surf zone/sea.

The behavioural repertoire of seals was divided into mutually exclusive categories described by Stirling (1971), Crawley, Stark & Dodgshun (1977) and Johnstone & Davis (1987). These included 'Lying and Alert' (together forming the Inactive category), interacting with adult males (AM), adult females (AF), subadults (SA) and 'Other' which includes walking and grooming (together forming the Active category). Activities/non-activities were scored separately for the dry hauling ground (beach) and surf zone (defined as the area which is wet as a result of wave action). Adult males were accorded the most attention, since they are conspicuous, present in high numbers in all three colony types, and since predictions could be made for their activity patterns based on the age/sex composition of the colonies. The percentage of animals engaged in a particular behaviour was used as an estimate of the percentage of time spent on that activity by an individual. Differences between groups of seals in the allocation of time were examined by Chi-square analysis of the original number of observations recorded.

Results

Diurnal haulout and departure patterns

A. tropicalis at the non-breeding colony site showed a haulout peak during the period 09:00 – 10:00 with a general decrease towards 16:00 (Figure 1). Most departures occurred from 09:00 – 13:00, with a decline in the departure rate thereafter. The greatest number were present ashore between 10:00 and 11:00 (n = 2 days) or 14:00 – 15:00 (n = 1 day) with concomitant lowest counts at midday and during the morning. Different temperature regimes on two different days at the non-breeding colony site had different influences on the number of fur seals ashore (Figures 2 & 3). Smallest numbers were present at high ambient temperatures (Figure 2). Onshore numbers of adult males as a class varied continually when high ambient temperatures prevailed (Figure 4). All but two clearly territorial males occupying territories on the waterline, departed at least once, resulting in a net loss of males by 16:00. Rates of departure and arrival were highest after 11:00, resulting in a definite drop in numbers ashore by 13:00. On the other hand, *A. tropicalis* territorial males in breeding colonies only resorted to the sea under high environmental temperatures when no females were present in their territories, and they invariably returned during the same day.

Social interactions

The majority of interactions (n = 802) on the dry hauling ground at the non-breeding colony site (during 51 h of

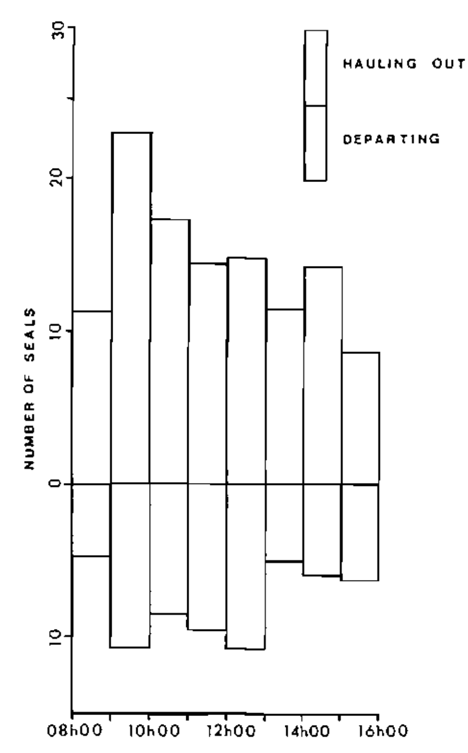

Figure 1 Combined results (hourly average) of seals hauling out on to, and departing from a non-breeding colony site on four days from 08:00 – 16:00.

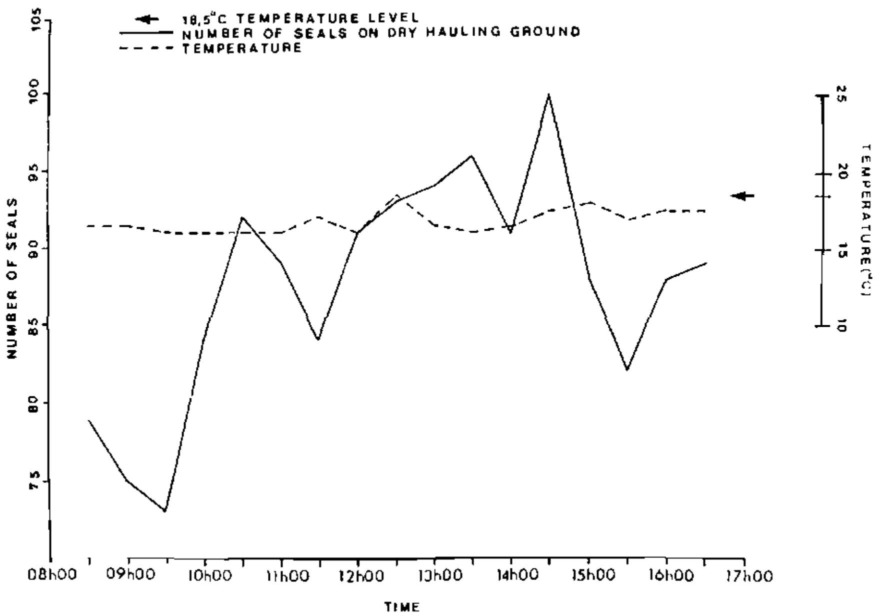

Figure 2 Changes in the number of fur seals on the dry hauling ground at a non-breeding colony site during a day with ambient temperatures ≤18,5°C.

observation spanning eight days between 20.11.1974 and 17.02.1975) involved at least one member of the subadult class (95,6%) with 77,2% of interactions taking place between subadults. Adult male participation was low, directed mostly at the boisterous subadult class (18,0%), with only 3,5% of interactions being recorded between adult males. Involvement with the few adult females present was negligible.

The diurnal rhythm in interaction frequency on the dry hauling ground was highest from 08:00 – 09:00 with a reduction towards midday followed by an increase for the period 14:00 – 16:00 (Figure 5). Despite smaller numbers of seals in the surf zone than on the dry beach, 65,0% of a noted 2290 social interactions was scored here. On average 0,618 interactions were recorded per individual at each scan of seals in the surf zone compared with only 0,045 on the dry zone and the difference was significant (χ^2_1 = 27 646, p < 0.001). The difference in interaction frequencies in these two zones is especially evident during midday hours (Figure 6) when surf zone interactions peak and dry zone interactions reach a concomitant low.

Activity in the non-breeding colony, as measured by the frequency of social interactions, increased greatly in the surf zone at ambient temperatures exceeding the 'comfortable' threshold value of 18,5°C (Figure 7). The number of interactions also increased on the dry hauling ground, but

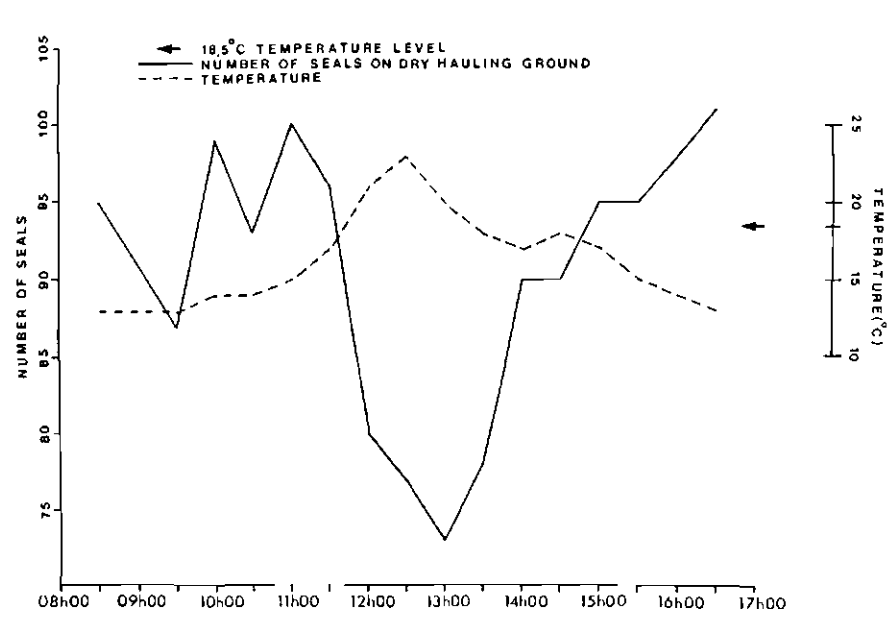

Figure 3 Changes in the number of fur seals on the dry hauling ground at a non-breeding colony site when ambient temperatures exceeded 18,5°C.

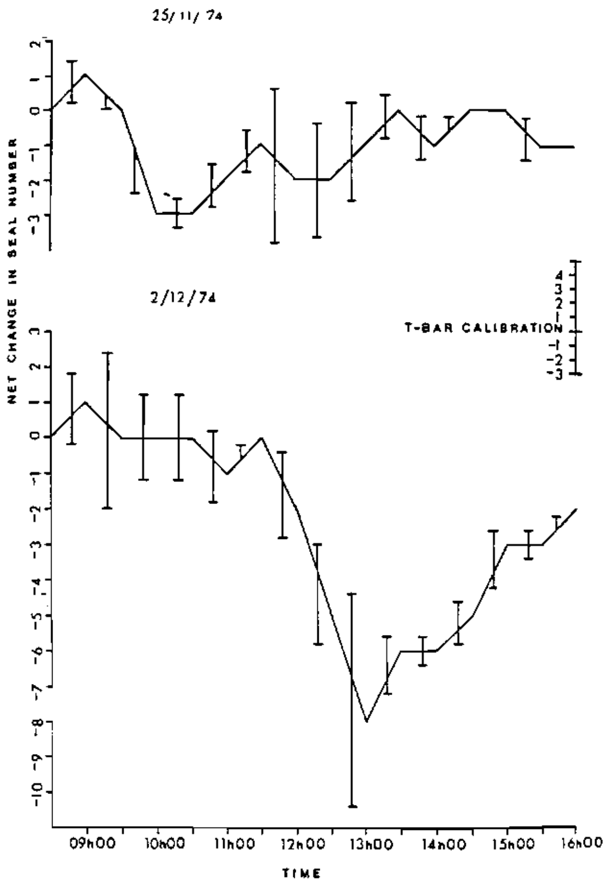

Figure 4 Net change in numbers of adult males at a non-breeding colony site with t-bars showing the change in numbers ashore for each half-hour interval. Ambient temperatures were already limiting at the start of the observation periods.

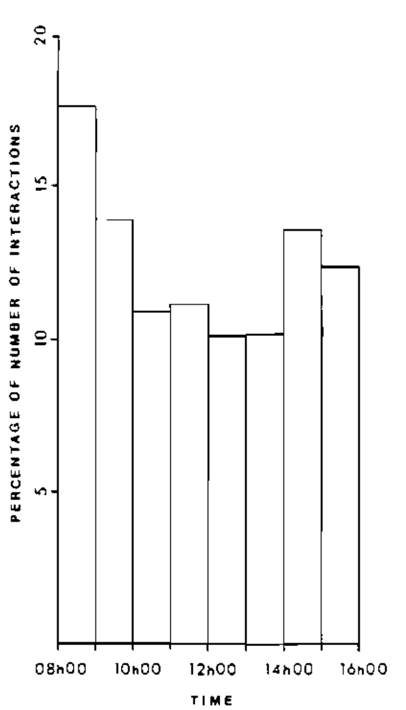

Figure 5 Diurnal rhythm in interaction frequency of fur seals on the dry hauling ground at a non-breeding colony site, based on observations from 08:00 – 16:00 on six days, and expressed as a percentage of the total number of interactions scored (n = 734).

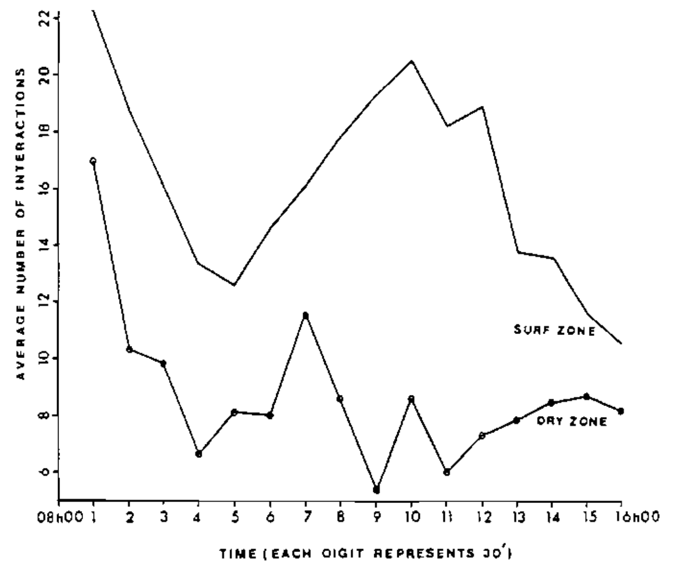

Figure 6 Mean number of interactions scored for each half-hour period from 08:00 – 16:00 on seven days of observation in the surf zone and dry hauling ground respectively, at a non-breeding colony site.

remained smaller than in the surf zone except at lower temperatures. Rain of considerable quantity and intensity, especially at its outset, effectively reduced the interaction rate of seals in the dry zone (Figure 7). A soft drizzle throughout the day did not elicit such a definite response.

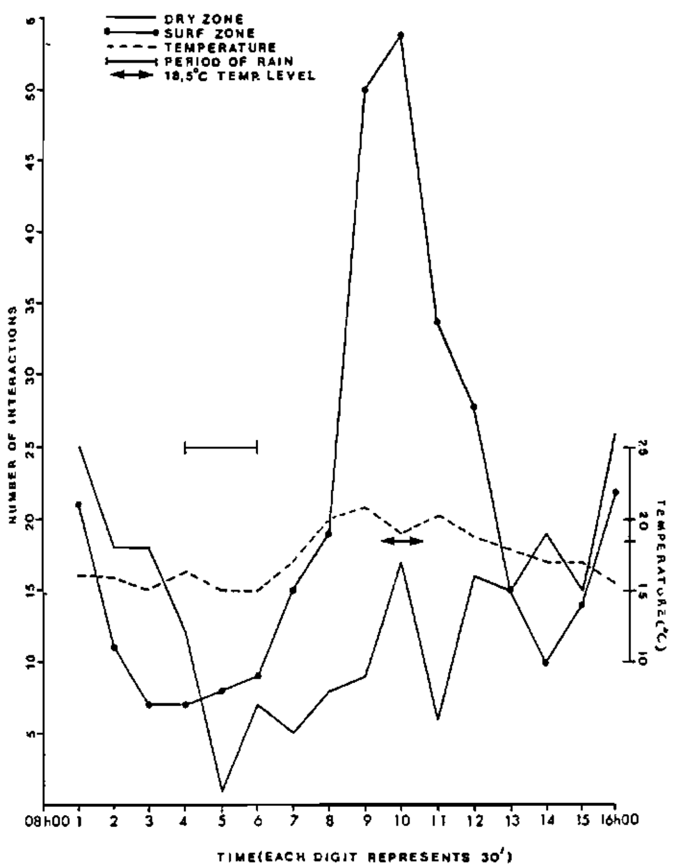

Figure 7 The influence of temperature on the number of social interactions in *A. tropicalis* at a non-breeding colony site for the period 08:00 – 16:00 on 20.12.1974.

Table 1 Time (%) allocated to different behaviours by adult male fur seals observed for 17 days during the austral summer at idle (n = 3110 observations), non-breeding (n = 5475 observations) and breeding (n = 4744 observations) colony sites

		Categories of behaviour					
		Inactive		Active			
Colony type	Observation time (h)	Lying %	Alert %	AM:AM %	AM:AF %	AM:SA %	Other* %
Idle	23	97,2	0,7	0,3	0	0	1,9
Non-breeding	90,3	89,0	4,4	0,7	0,2	4,0	1,8
Breeding	33,3	81,1	12,1	1,2	3,2	1,3	1,1

* Locomotion and grooming

Time budgets

Idle adult males had a high inactivity rate, showing little interest in their surroundings which they shared with the larger range of subadult males. No territories were defended, 97,0% of the time was spent inactive in the lying down and alert positions (0–01%) with non-social activities (grooming and locomotion) dominating periods of activity (Table 1). Adult males at non-breeding colony sites, where at least some defend territories, showed increased activity through involvement with the few adult females and numerous subadult males present. They were also more alert than idle adult males (χ^2_1 = 89,4; p < 0,001). Despite a high incidence of inactivity, territorial males in breeding colonies spent significantly more time alert than those in non-breeding colonies (χ^2_1 = 177,1; p < 0,001) and most active time was spent interacting with adult females (3,18%). Inter-male interaction, as an expression of vigorous territorial maintenance, increased more than that of adult males in non-breeding (χ^2_1 = 4,97; p < 0,05) and idle (χ^2_1 = 15,8; p < 0,001) colonies.

Adult males on a particular site showed considerable variation in activity levels. For example, on 25 November 1974, 66% of all interactions by adult males involved only two of the average of nine males under observation from 08:00 – 16:00. On 2 December 1974, two of an average of 23 males observed were responsible for 42% of all interactions logged. On both days the active males occupied frontline territories.

On the dry hauling ground in the non-breeding colony the subadult class spent significantly (χ^2_1 = 234,5; p < 0.001) more time active (15,3%) than adult males (6,7%), chiefly as a result of peer group involvement (10,2%) and non-social activities (4,8%). Increased activity, in particular grooming and movement to and from the sea/surf zone, was evident during the higher range of temperatures (Table 2). Time budgets of subadults (Table 3) further show that at any time during the day individuals in the surf zone are significantly more active than those on the dry zone (χ^2_1 = 1525,9; p < 0.001).

Table 2 Time (%) allocated to different behaviours by adult male (n = 5475 observations) and subadult (n = 8650 observations) fur seals on the dry hauling ground at a non-breeding colony site

Behaviour	Males	Subadults	χ^2_1
Lying	89,0	82,3	9,4; p < 0,005
Alert	4,4	2,5	37,1; p < 0,001
AM	0,7	0,2	21,0; p < 0,001
AF	0,2	0,0	
SA	4,0	10,2	155,8; p < 0,001
Other*	1,8	4,8	83,7; p < 0,001

* Locomotion and grooming

Discussion

At the non-breeding colony site, the hauling-out rate of *A. tropicalis* is high during the morning. Towards the afternoon maximum, or near maximum, numbers are attained onshore which accords well with the peak in New Zealand fur seals *A. forsteri* during the late afternoon (Stirling 1968; Crawley 1972). The fur seals also leave the beach throughout the day, usually at a lower rate, resulting in a net gain in numbers ashore (present study). The small numbers ashore during the morning suggest a net loss during the evening and night which might be associated with nocturnal feeding (Bester & Laycock 1985). This suggests that the 'energy

Table 3 Time budget of subadult fur seals on the dry hauling ground and surf zone respectively, for four random hours of observation on three days at a non-breeding colony site

	Dry zone		Surf zone		Mean number of seals present	
Date	Active %	Inactive %	Active %	Inactive %	Dry zone	Surf zone
7.11.75	16,8	83,1	67,9	32,1	69,5	12,5
12.11.75	6,8	93,1	76,9	23,1	50,6	24,3
14.11.75	4,2	95,8	88,7	11,4	74,5	14,2
Mean	11,4	88,6	76,0	24,0	66,0	15,9

conservation' hypothesis is, as predicted, probably not relevant at non-breeding colony sites since idle adult males may leave at least temporarily to feed.

The reversal of the hauling-out and departure rates of the fur seals under conditions of high ambient temperatures during the day suggests that, while the species can cope with thermal loading under moderate conditions, the ultimate response to excessive solar radiation and high environmental temperatures is movement to the surf zone and the shallows/sea. This is evident during midday hours when high temperatures prevail, especially when a threshold value of 18,5°C is exceeded, and indicates that the limits to which their physiological and behavioural mechanisms can extend their thermal tolerance have been exceeded (Fay & Ray 1968).

The exodus is conspicuous at non-breeding colony sites where all age classes are involved (this study) and for adult females at breeding colony sites (Bester 1977), as also seen in *A. forsteri* (Gentry 1973; Miller 1974). At non-breeding colony sites temperature-induced departures of adult males are common and a result of relaxed territorial control in the absence of females (this study). Territorial males at breeding colony sites, away from the water-line and without the added incentive to remain when without females in their territories, are also more likely to respond by temporarily abandoning these territories, similar to other breeding male otariids (Bartholomew & Wilke 1956; Rand 1967; Gentry 1973), when thermoregulatory behaviour overrides reproductive activities (Whittow 1987). The migration onto the surf zone and into the sea by the fur seals suffering heat stress suggests that they take advantage of the favourable temperature gradient that exists for heat loss, the increased interaction rate in the surf zone resulting from the increased population pressure there.

High ambient temperatures in conjunction with high solar radiation markedly influenced the activity patterns of *A. tropicalis* at non-breeding and idle colony sites, specifically since lack of involvement with territories or breeding allows the fur seals to respond readily to heat load. The diurnal rhythm in interaction frequency on the dry hauling ground followed the hauling and departure rate of the fur seals, with peaks associated with high turnover ashore (morning) or increased density (afternoon). The low interaction frequency around noon relates to higher ambient temperatures, as in *A. forsteri*, where the herding behaviour of territorial males is depressed at high temperatures (Miller 1974), and *Callorhinus ursinus*, which responds to an increase in environmental temperatures with a decrease in general activity (Bartholomew & Wilke 1956). The marked higher activity level in the surf zone, on the other hand, is related to the favourable temperature gradient. Perhaps significantly, most active adult males on non-breeding colony sites occupy foremost territories situated on the water-line, an area favoured by all age/sex categories when high ambient temperatures prevail and subjected to the movement of arriving and departing seals throughout the day. *A. forsteri* males are also relatively inactive during the hot midday except for those positioned on the water-line (Miller 1974).

Although the interaction rate declined on the dry hauling ground at high temperatures, the increase in activity resulted chiefly from the movement of seals to and from the water. In addition, the increase in the per cent time spent grooming is also linked to the movement between surf zone and dry hauling ground. Grooming is a normal reaction of *A. tropicalis* after immersion in water and most extensive grooming in *A. forsteri* generally took place immediately after the seal left the water (Stirling 1970). The increase in the grooming action is also evident during periods of prolonged rain or even after a short downpour (Bester 1977). The initial depression of the interaction rate is probably the result of discomfort caused by the percussive effect of the raindrops (Bonner 1968).

It can be concluded that the daily change in numbers ashore, the relative contribution of the different age and sex classes, their location and distribution on site, and prevailing weather conditions clearly influence the pattern of interaction and allocation of time to the various activities in *A. tropicalis*. The overall picture for all age classes is high inactivity, which is particularly evident in adult males, idle or territorial, and is matched by the behaviour in other pinnipeds (Stirling 1971; Crawley *et al.* 1977; McCann 1983; Anderson & Harwood 1985).

Time allocation patterns in this study seem to accord with the conclusions on the effects of finite resources on behaviour reached by the majority of studies (Stirling 1971; Sandgren 1976; Crawley *et al.* 1977; Anderson & Harwood 1985), although Miller (1971) and Boness (1984) thought it unlikely that a territorial male's reserve affects its activity budget. Boness (1984) did not allow for a relationship between size and sexual success (Anderson & Harwood 1985), and Miller (1975) considered the relationship between large body size and the ability to fast for prolonged periods probably of secondary importance among territorial male fur seals.

Large adult *A. tropicalis* males at idle and non-breeding colony sites in this study expend little energy but do not enhance their opportunities to mate and contribute to the gene pool — this would require relocation to breeding colony sites. Since activity consistently results in an increase in core body temperature of pinnipeds (Bartholomew & Wilke 1956; McGinnes & Southworth 1967; Whittow *et al.* 1975), and since sea lions that sleep (engendering a substantial reduction of metabolic heat production and body temperature — Matsuura & Whittow 1973) during exposure to heat are likely to be more tolerant than those that are awake (Whittow *et al.* 1975), it is suggested that *A. tropicalis* reduces the risk of over-heating by inactivity. As this affects adult males whatever their status (93,2 – 97,9% of time spent inactive) in a species where local distribution is also affected by thermoregulatory considerations (Bester 1982a; 1982b), this study suggests that inactivity is a behavioural characteristic which serves a dual purpose. Inactivity first and foremost reduces endogenous heat-loading in response to proximate environmental stimuli in the absence of a favourable heat loss gradient, and secondly, reduces energy expenditure. Both factors seem to be important in the ability of males to maintain their position on a beach for protracted periods during the breeding season.

Acknowledgements

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