SOCIAL BEHAVIOUR OF JACKASS PENGUINS AT SEA

W. R. SIEGFRIED, P. G. H. FROST, J. B. KINAHAN & J. COOPER
FitzPatrick Institute, University of Cape Town

ABSTRACT

This paper reports flocking, communal feeding and other aspects of sea-based social behaviour in the jackass penguin (*Spheniscus demersus*). Penguins tend to occur within about 15 km of the mainland, but range farther afield from the islands used for breeding and/or roosting. Relatively large groups of 50 and more birds occur more than 50 km from the nearest island, but seldom more than 15 km from the mainland. The majority of the sea-going population consists of birds occurring in groups. Mean group size is eight birds. In any one particular group the members all tend to perform the same behaviour at the same time. The tendency to form foraging groups and the highly synchronized diving and cohesion of these groups indicate that this behaviour is socially facilitated, suggesting that it is adaptive in terms of both enhanced prey location and capture. Feeding penguins do not submerge for long and do not dive deeply. Birds in diving groups perform head-dipping movements which might signal readiness to dive and thus promote synchronous activity. The paper points out how little is known about jackass penguins at sea – the environment in which they probably spend the majority of their time. Lack of information on the birds at sea precludes proper interpretation of many land-based events attending the biology of the bird and its conservation.

INTRODUCTION

Penguins are highly social in all breeding and non-breeding activities. Flock behaviour has been studied on land and pack-ice (Ainley 1972), but flocking of penguins at sea has received scant attention. In particular, little is known about their feeding behaviour (Kooyman 1974). The present report deals with flocking, communal feeding and other aspects of sea-based social behaviour in the jackass penguin (*Spheniscus demersus*) which is restricted to southern African seas (McLachlan & Liversidge 1970). The paper emphasizes how little is known about the species at sea, even concerning the general topics treated below.

During 1954–1960 the South African Government Research Vessel R.S. *Africana II* made monthly cruises in the neighbourhood of St. Helena Bay (for positions of cruise stations see Marchand 1952). On several stages of the cruises regular bird-watches were carried out. Records were kept by Cdr. A. Thomas, and during 1956–1957 by one of us (W.R.S.). Additional data for 1958–1968 were made available by Mr. P. Zoutendyk who recorded sea-birds whilst cruising with the University of Cape Town's Research Vessel *T. B. Davie* (Zoutendyk 1965).

Since 1970 we have recorded penguins during boat trips between Cape Town, Dassen Island and Saldanha Bay. Observations from vantage points on land were made at Cape Point, Dassen Island, Marcus Island, South Head and Bird Island, Lambert's Bay. These places and the area covered by the sea-cruises are shown in Figures 1 and 2. Table 1 lists all breeding sites (all are islands) and their populations of jackass penguins within the area covered by the survey cruises.

TABLE 1

Jackass penguin breeding and/or roosting islands within the area covered by the survey cruises

Roosting and/or breeding island	*Distance island from mainland (km)*	*Current estimates for population of penguins**
Bird Island	0	500
Dassen Island	8	70 000
Vondeling Island	1	400
Saldanha Bay islands:		
Jutten	1	7 000
Marcus	1	6 000
Malagas	1	1 000
Seal Island	5	150
Dyer Island	4	38 000

* Excludes nestlings.

DISTRIBUTION AT SEA

Tables 2 and 3 summarize data on occurrence and abundance of jackass penguins at sea. The birds tend to occur within about 15 km of the mainland, but range farther afield from the islands used for breeding and/or roosting. Rand (1960) has shown that the birds are not restricted to special inshore feeding grounds, but are scattered over all 350 km of coast between Lambert's Bay and Dyer Island, and usually keep well away from the rocky coast. Relatively large groups of 50 and more birds occur more than 50 km from the nearest island, but seldom more than about 15 km from the mainland.

Although surveys were made in all months of the year, the data are insufficient to permit detailed, definitive analysis for seasonal variation in the distribution and abundance of penguins at sea. Apparently, however, the overall pattern changes very little from one month to the next, and there are always substantial numbers and large groups of birds ranging relatively far from their breeding and/or roosting islands. This may be related partly to young birds delaying for two years the onset of breeding, and older birds breeding in all months of the year (Rand 1960; our unpublished data).

While the majority of the sea-going population consists of birds occurring in groups, we know little about the composition of these groups in terms of age and sex of the birds. Table 4 indicates that immature birds tend to be members of relatively large groups, returning to land after foraging at sea.

Jackass penguins, as solitary individuals or in groups, are observed regularly at sea during the hours of darkness. However, we cannot say what time is spent, either continuously or in broken periods, at sea by non-breeding or non-moulting birds. Nor can we say whether group size at night differs from that observed during daytime.

TABLE 2

Per cent frequency of occurrence and per cent numerical abundance (figures in italics) and mean group size (S.D. and range) of jackass penguins at sea in relation to distance from nearest mainland and breeding and/or roosting island

	kilometres										
Nearest mainland	*0–12*	*13–24*	*25–36*	*37–49*	*50–74*	*75–99*	*100–124*	*125–149*	*150–190*	*No. penguin sightings*	*No. penguins*
% occurrence	44	15	18	10	13	6	3		1	163	
% abundance	*79*	*7*	*5*	*2*	*5*	*1*	*0,5*		*0,5*		1 596
Mean group size	14±30 1–200	10±10 1–30	3±5 1–20	3±3 1–8	4±4 1–15	3±2 1–7	2±1 1–7		1 1		
No. observation stations	201	78	122	89	171	102	107	22	91		
Nearest island											
% occurrence	33	38	32	30	16	5	12	5	4	163	
% abundance	*8*	*11*	*18*	*32*	*25*	*2*	*3*	*0,5*	*0,5*		1 596
Mean group size	11±11 2–40	8±22 1–100	9±19 1–90	16±39 1–206	10±20 1–100	4±3 1–8	3±4 1–15	1 1–2	1 1–2		
No. observation stations	36	52	93	107	242	122	132	65	134		

TABLE 3

Group size of jackass penguins observed at sea

Group size	*1*	*2–5*	*6–10*	*11–20*	*21–50*	*51–210*
Number groups	82	113	44	19	15	9
Per cent frequency	29	40	16	7	5	3

BEHAVIOUR AT SEA

During daytime sea-going jackass penguins, as solitary individuals or in groups, forage, swim, rest, bathe and perform additional comfort behaviour. Table 3 embraces all birds seen at sea. Based on these data, mean group size is eight birds. However, unless the observer's ship is stationary or is situated a fair distance from the penguins under observation, it is difficult to classify the birds definitively according to their behaviour. Thus, Table 5 embraces a relatively small sample of birds known to have been undertaking certain behaviour. In any particular group the members all tend to perform the same general behaviour at the same time. These behaviour patterns all occur in both small and large groups located at all distances from the nearest breeding and/or roosting island.

Ainley (1974) observed that Adélie penguins (*Pygoscelis adeliae*) bathe only when in flocks; and that bouts of bathing are of short duration and are delayed in onset until the birds are well beyond the surf fringing a beach. Ainley suggested that this behaviour is socially facilitated and that it is adaptive as an anti-predator strategy. The jackass penguin behaves differently, and this might be due to different and relatively lower predation pressures believed to be operating on the species (Cooper 1974).

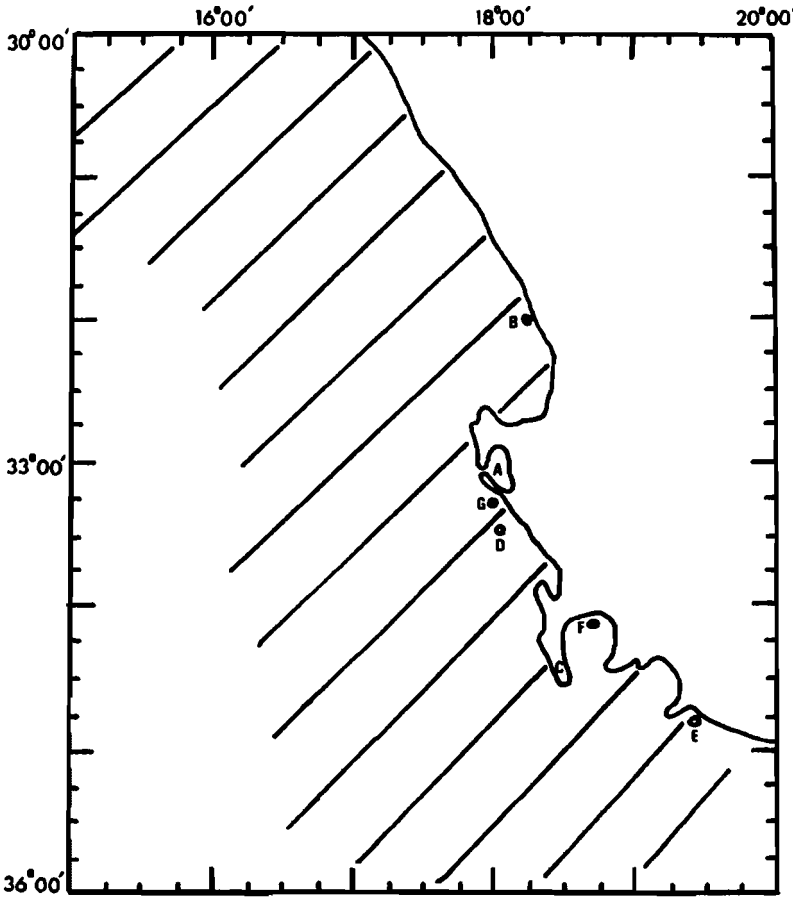

FIGURE 1

The region of sea (hatched) covered by the survey cruises. (A) Saldanha Bay; (B) Bird Island, Lambert's Bay; (C) Cape Point; (D) Dassen Island; (E) Dyer Island; (F) Seal Island; (G) Vondeling Island.

Jackass penguins leaving land do not delay onset of bathing until well beyond the surf. Instead, the birds tend to join and form large bathing flocks usually 5–10 metres from a landing beach (Frost, Siegfried & Burger in press). These flocks are comprised of birds about to depart on foraging journeys, and of temporarily land-based birds either breeding or moulting. Once having completed their bathing, birds intent on making foraging journeys depart in groups from the large flocks and swim out to sea with individuals making relatively few, and then only brief, attempts to bathe (Tables 6 and 7). Groups returning to rookeries after spells at sea are significantly smaller ($P < 0{,}001$) than groups setting out on foraging journeys (Table 8).

Flocks of sea-going jackass penguins respond to disturbance by: "sounding"; remaining on the surface while swimming away; and, "porpoising" (Frost, Shaughnessy, Semmelink,

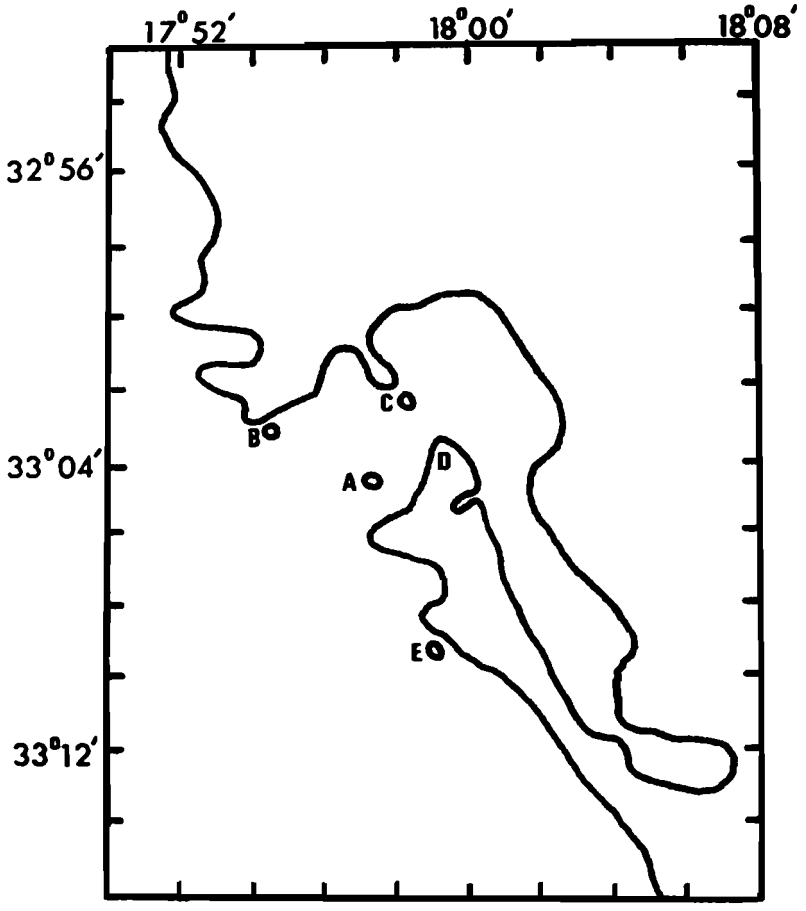

FIGURE 2
Saldanha Bay and environs. (A) Jutten Island; (B) Malagas Island; (C) Marcus Island; (D) South Head; (E) Vondeling Island.

Sketch & Siegfried 1975). Normally the behaviour of birds in such flocks is well synchronized, but we know very little about the communication methods promoting this. Observations and studies are needed to elucidate the significance of passive sonai (Poulter 1969) and vocalizations as social signals. Jackass penguins utter loud calls when panicked into porpoising (pers. obs.). and have been recorded vocalizing in fog (Thomas in litt.) and during dark nights (pers. obs.) when far out at sea. Stonehouse (1967) mentions that sea-going *Aptenodytes* and *Pygoscelis* penguins utter loud vocalizations, as distinctive rallying calls which facilitate flocking.

It is not known whether jackass penguins forage at night, nor whether they indulge in any nocturnal activities other than either swimming or resting, or both, on the surface of the sea. However, Rand's (1960) observations indicate that feeding is essentially a diurnal activity. We know nothing about the frequency or duration of foraging bouts.

TABLE 4

Mean group size, according to presence and absence of immature birds, of jackass penguins returning to Dassen Island after journeys at sea in November

Groups comprising							
Adult birds only				*Adult and immature birds*			
$\bar{X}$	*SD*	*range*	*n*	$\bar{X}$	*SD*	*range*	*n*
4,2*	3,6	1–17	216	8,5*	7,9	1–35	54

* The means are significantly different $P < 0{,}001$.

TABLE 5

Number groups of jackass penguins in relation to their behaviour at sea

	Group size					
Behaviour	*1*	*2–5*	*6–10*	*11–20*	*21–50*	*51–210*
Resting	8	10	3	1	2	3
Swimming	12	21	7	3	1	1
Bathing & preening	13	5	8	3	1	
Foraging (diving)	27	20	13	6	2	

TABLE 6

Frequency and duration of bathing by jackass penguins swimming a measured 200 m out to sea after departure from a main bathing flock 5–10 m from a landing beach

Groups of birds				*Birds in groups*	
No. observed	% *with birds bathing*	*Duration of observation (minutes)*	% *time spent bathing*	*No. observed*	% *bathing*
43	58	144	6	537	21

TABLE 7

Incidence of bathing jackass penguins in relation to distance they move seawards from a main flock 5–10 m from a landing beach

	Distance (metres) extending out to sea from main bathing flock				*n*
	0–50	*51–100*	*101–150*	*151–200*	
% groups bathing	77	12	7	4	40 groups
% birds bathing	67	14	12	7	112 birds
% time spent bathing by groups	67	20	9	4	499 seconds

TABLE 8

Mean group size of jackass penguins in relation to their arrival at or departure from Dassen Island in November

Arrival from sea				*Departure for sea*			
$\bar{X}$	*SD*	*range*	*n*	$\bar{X}$	*SD*	*range*	*n*
4,8	4,5	1–26	260	11,2	7,5	1–56	134

Jackass penguins forage by diving, but we do not know at what depths the birds capture their prey. Cephalopods and pelagic shoaling fish, mainly juveniles, comprise the principal food of the species (Davies 1955, Rand 1960). Kooyman (1975) rightly cautions against making too much out of the type of food eaten as a guide to diving depth in penguins, because so little is known about the habits of the species preyed upon. Judging from the length of the dives (Table 9), jackass penguins generally do not submerge for long and it seems reasonable to infer that they do not dive deeply. Obliquely slanted dives and underwater swimming in the horizontal plane, presumably in pursuit of fast-moving prey, are usual rather than vertical plunges and the birds surfacing where they dived initially.

We know little about speeds achieved while travelling under water or on the surface. Davies (1955) thought that 4–5 knots might represent the species' normal cruising speed. Birds in groups heading out to sea, after leaving a beach/bathing flock, proceed by synchronized and alternating bouts of under-water and surface swimming. These birds tend to travel at about the same speed irrespective of group size (Table 10). Birds returning from journeys at sea tend to progress by porpoising rapidly over the last few hundred metres to the beach. Table 11 gives data on speeds of travel of jackass penguins arriving at, or departing from, a landing beach at Dassen Island. It is evident that the mean speed of incoming birds significantly exceeds mean speed of outgoing birds.

TABLE 9

Mean time under water per dive and mean pause time on surface between dives in jackass penguins foraging at least 500 m offshore of nearest land

No. of birds in group	*Time (seconds) under water*				*Time (seconds) on surface*			
	$\bar{X}$	*SD*	*range*	*n*	$\bar{X}$	*SD*	*range*	*n*
1	17,6	10,8	5–37	14	15,7	7,9	2–32	15
2–3	24,1	11,2	7–48	42	18,6	13,4	3–48	46
4–5	20,4	6,9	8–34	31	17,5	10,4	4–42	31
6–9	23,0	6,9	17–32	4	19,1	12,4	5–37	9
10–14	18,8	2,6	16–21	3	—	—	—	0

TABLE 10

Mean speed of travel, number of dives, times underwater and on surface in groups of jackass penguins swimming a measured 200 m out to sea after departing from a main bathing flock 5–10 m from a landing beach

No. birds in group	*Speed (km/hr)*	*No. dives*	*Time underwater (secs)*	*Time on surface of water (secs)*	*No. groups observed*
2–6	3,5 ± 0,5	3,6 ± 1,1	99 ± 33	113 ± 40	8
7–11	3,5 ± 0,3	3,6 ± 1,0	94 ± 32	115 ± 34	14
12–16	3,6 ± 0,3	3,6 ± 1,0	93 ± 31	105 ± 37	6
17–21	3,9 ± 0,4	3,1 ± 1,1	60 ± 40	126 ± 51	7
22–27	3,9 ± 0,3	3,0 ± 0,4	51 ± 27	133 ± 40	3

TABLE 11

Swimming speeds of jackass penguins arriving at or departing from a landing beach. The birds were timed while swimming a measured 200 m

	Speed of travel (km/hr)			*No. groups of birds observed*
	$\bar{X}$	*SD*	*range*	
Arriving	6,2	0,8	4,8–7,2	10
Departing	3,6	0,5	2,9–4,8	43

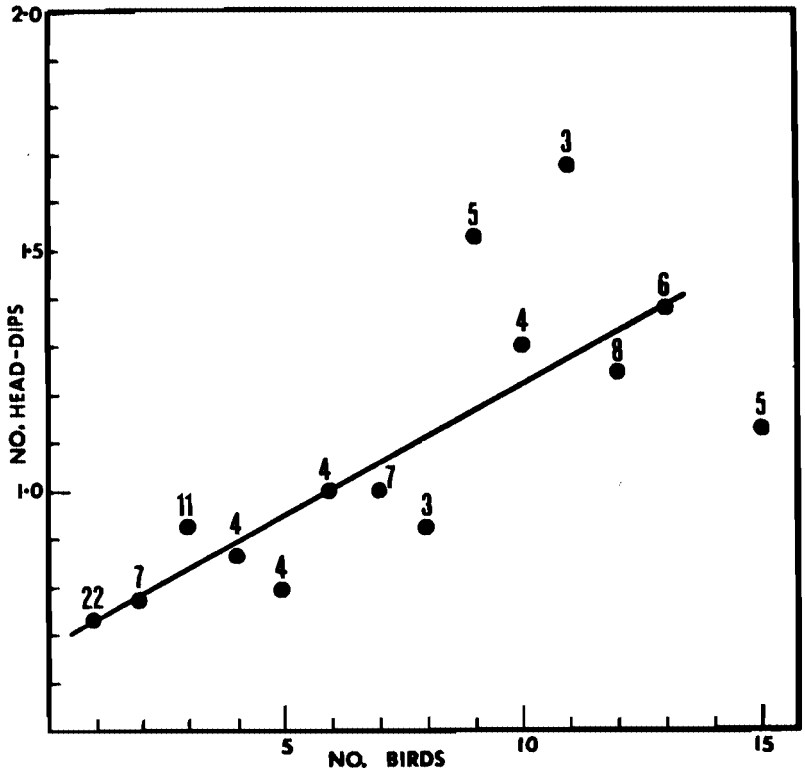

FIGURE 3
Mean number head-dipping movements per bird in foraging groups of different sizes. Observations of birds are individually numbered. Line fitted by eye.

The largest group observed actively foraging consisted of 42 members. These birds behaved as a rather synchronous group. Tables 12 and 13 summarize data on the degree of synchrony affecting the activity and spacing of penguins in foraging groups. It is evident that a relatively short time separates the first and last birds diving in groups of different size. Apparently the birds are grouped somewhat closer together on surfacing from a dive than just before submergence. Limited observations made from a raised promontory indicate that diving birds tend to "fan out" underwater and then regroup during and just after surfacing.

Preparatory to diving, foraging jackass penguins normally perform a varying number of head-dipping movements; the swimming bird thrusts its head and neck underwater, moving the head from side to side, usually for 1–2 seconds (Tables 14, 15 and 16). It is evident that the number of head-dips performed by individuals increases with increasing flock size (Figure 3). Individuals in large groups apparently keep their heads under longer than those in small groups (Table 15). While head-dipping very likely functions in assisting the bird to locate its prey we suggest that it might also have social significance in signalling readiness to dive and thus promoting synchronous activity.

TABLE 12

Temporal and spatial relationship between jackass penguins in foraging groups diving in *ca.* 15 m of water 60 m offshore of Dassen Island

No. of birds in group	*Time (seconds) elapsed*						*Nearest neighbour distance (m)*					
	between first and last bird diving			*between first and last bird surfacing*			*between birds just prior to diving*			*between birds on surfacing*		
	$\bar{X}$	*SD*	*n*	$\bar{X}$	*SD*	*n*	$\bar{X}$	*SD*	*n*	$\bar{X}$	*SD*	*n*
2–3	2,1	1,4	3	2,2	1,2	3	1,2	0,8	5	0,3	0,2	3
4–6	2,6	0,7	9	2,8	1,9	6	0,4	0,4	10	0,3	0,2	8
7–9	3,1	1,8	15	2,5	1,2	8	0,5	0,3	15	0,4	0,3	11
10–12	5,9	3,9	13	3,4	2,1	6	0,4	0,4	14	0,4	0,3	13
13–15	6,8	7,2	15	3,2	0,8	6	0,4	0,4	15	0,3	0,2	13
16–18	3,5	1,9	6	2,4	1,9	2	0,4	0,4	8	0,4	0,4	4
19–21	3,3	1,1	2	4,1		1	0,6	0,5	2	0,3		1
22–24	3,6	2,2	2	4,6		1	0,7	0,3	2	0,5		1
25–27	4,9	2,2	3	3,4	0,3	2	0,7	0,5	3	0,4	0,1	2

TABLE 13

Mean time elapsed between first and last bird diving in groups of foraging jackass penguins farther than 500 m from nearest land

No. birds in groups	*Time (secs)*			
	$\bar{X}$	*SD*	*range*	*n*
2	0,9	0,4	0–1,6	8
3	1,8	0,7	1,0–3,5	13
4	1,6	0,7	0,8–2,7	9
5	2,4	1,2	1,1–4,7	7
6	2,2	0,3	1,7–2,5	5
7	0,8	0,3	0,6–1,1	2
8	1,9	0,9	0,9–3,2	7
9	1,8	0,4	1,2–2,3	9
12	2,4	2,0	1,1–6,0	5

TABLE 14

Temporal incidence of head-dipping behaviour in jackass penguins foraging at least 500 m offshore of nearest land

No. birds in group	Time (secs) between first bird surfacing and first bird performing head-dipping				Time (secs) between first bird head-dipping and last bird diving			
	$\bar{X}$	SD	range	n	$\bar{X}$	SD	range	n
1	10,6	5,8	3–19	11	9,0	5,8	4–18	10
2–3	15,0	11,5	2–38	36	12,5	6,4	5–28	11
4–5	15,5	11,2	3–38	22	12,1	10,9	4–37	8
6–9	8,8	6,0	4–21	7	8,2	4,6	3–16	6

TABLE 15

Duration of individual head-dipping movements performed by jackass penguins foraging at least 500 m offshore of nearest land

No. birds in groups	Time (secs) individual head-dips			
	$\bar{X}$	SD	range	n
1	1,0	0,8	0,1–2,0	4
2–3	1,4	1,4	0,2–4,1	22
4–5	1,0	0,8	0,2–2,2	10
6–7	1,6	1,5	0,3–4,1	5
8–10	1,8	1,8	0,2–5,1	6

The tendency to form foraging bands and the highly synchronized diving and cohesion of these groups indicate that this behaviour is socially facilitated, suggesting that it is adaptive in terms of both enhanced prey-location and capture. However, we know very little about how penguins capture prey. According to Rand (1960) bands of penguins attack prey without any co-ordination or scheme of hunting, but attacks on fish are apparently made from below a shoal, presumably because this offers the penguins a wider choice of prey than would be the case in attacking from the side. The fact that penguins swallow their prey under water makes it difficult to determine the degree of success attending prey-capture, though from the weight of food found in stomachs, Rand (1960) postulated that the birds hunt equally well alone and in large groups. This requires investigation.

Even less is known about how jackass penguins locate their prey. Poulter (1969) suggested that penguins use cavitation "clicks" as a source of passive sonar to aid in locating prey under conditions of reduced visibility. However, in the jackass penguin auditory acuity, measured in

TABLE 16

Mean number head-dipping movements performed in groups of jackass penguins foraging at least 500 m offshore of nearest land

No. birds in group	*Number head-dipping movements*			
	$\bar{X}$	*SD*	*range*	*n*
1	0,7	0,8	0–3	22
2–3	2,2	2,8	0–9	17
4–6	5,0	1,9	2–12	12
7–9	9,2	5,8	3–21	15
10–12	15,5	9,0	4–32	14
13–15	13,5	7,2	4–28	14
16–18	11,3	7,7	5–21	6
19–21	25,0	18,4	12–38	2
22–24	20,5	16,3	9–32	2
25–27	15,0	9,8	4–23	3

terms of cochlear potentials, declines rapidly at frequencies above 5 kHz, though some sensitivity to frequencies as high as 15 kHz remains (Wever, Herman, Simmons & Hertzler 1969). Thus if jackass penguins do use cavitation "clicks" as a source of passive sonar they must be responding to "clicks" in the lower range of frequencies that extends from 640 Hz to above 64 kHz. While low frequency "clicks" will be relatively less attenuated through the water, there is little doubt that any use of passive sonar by penguins can be effective only over short distances. Penguins must use other clues to locate fish shoals at sea.

Little is known about the spatial distribution of the shoals of young fish on which the jackass penguin feeds (Davies 1956 b, 1957). Do foraging bands of penguins encounter these shoals of pelagic fish merely by random chance? If not, and if their searching behaviour is non-random, what factors are responsible for this? Is the jackass penguin able to discriminate between water masses favourable or unfavourable for determining the positive incidence of shoals? Do the penguins follow, and are they attracted to, bands of feeding sea-birds such as Cape gannets (*Sula capensis*) and Cape cormorants (*Phalacrocorax capensis*)? Davis (1956 a) reports groups of penguins coming together when shoal fish are present, and that whenever a shoal is being "worked" by gannets and cormorants penguins are invariably present.

Nothing is known about possible intraspecific competition for feeding rights, though dominance-subordinate hierarchies might be predicted in penguin flocks, especially when the birds are concentrated to breed. Foraging distance and food-finding time must have relatively short limits for breeding penguins exploiting the supposedly patchily distributed shoaling fish around the islands used for nesting (Frost, Siegfried & Cooper in press).

Furthermore, virtually nothing is known about the effect of the modern fishing industry on the relative abundance and availability of these shoals to the penguin. Being flightless, and

consequently having a relatively restricted foraging range, penguins must be reliant upon a highly predictable rate of encounter with their mobile prey. Indeed, it is difficult to see how flightlessness could have evolved in the absence of a predictable temporal and spatial pattern of prey distribution. If the result of extensive commercial fishing is to reduce the size and frequency of occurrence of fish shoals, then we might predict that the concomitant decline in the rate of encounter between predator and prey will have an adverse effect on the jackass penguin. This presumed competition with the fishing industry is *thought* to be one of the factors contributing to a declining penguin population (Westphal & Rowan 1971, Frost *et al.* in press). However, until we understand the dynamics of this predator:prey interaction, we are in no position to fully evaluate the impact of the fishing industry on the penguin population.

CONCLUSIONS

The main purpose of this paper has been to point out how little is known about jackass penguins at sea – the environment in which they probably spend most of their time. Many land-based events attending the biology of the species, in particular its breeding success, will be interpreted fully only when more is known about the bird at sea. Such information is necessary to gain a better understanding of the species' population dynamics (Jackson, Siegfried & Cooper in press), and so contributing towards informed conservation-management of its declining population (Frost, Siegfried & Cooper in press).

ACKNOWLEDGEMENTS

This paper is one in a series reporting on a programme of research dealing with the ecology and conservation of the jackass penguin. The programme is supported financially by the National Geographic Society, The Witwatersrand Bird Club, the Oppenheimer Memorial Fund and the University of Cape Town. For logistical support and other assistance we are indebted to the Sea Fisheries Branch of the Department of Industries. One of us (J.C.) acknowledges the support he received from the South African Nature Foundation and the South African National Foundation for the Conservation of Coastal Birds. We thank Jane Dowle and Gill Puttick for contributing observations and for helping with the sorting of data.

REFERENCES

AINLEY, D. G. 1972. Flocking in Adélie Penguins. *Ibis*, 114:338–390.

AINLEY, D. G. 1974. The comfort behaviour of Adélie and other penguins. *Behaviour*, 50:16–51.

COOPER, J. 1974. The predators of the jackass penguin *Spheniscus demersus*. *Bull. Br. Orn. Club*, 94:21–24.

DAVIES, D. H. 1955. The South African Pilchard (*Sardinops ocellata*): bird predators, 1953–54. *Investl. Rep. Div. Fish. Un. S. Afr.* 18:1–32. Pretoria.

DAVIES, D. H. 1956a. The South African pilchard (*Sardinops ocellata*) and maasbanker (*Trachurus trachurus*): bird predators, 1954–55. *Investl. Rep. Div. Fish. Un. S. Afr.* 23:1–40. Pretoria.

DAVIES, D. H. 1956b. The South African pilchard (*Sardinops ocellata*): migration, 1950–55. *Investl. Rep. Div. Fish. Un. S. Afr.* 24:1–52. Pretoria.

DAVIES, D. H. 1957. The South African pilchard (*Sardinops ocellata*) and maasbanker (*Trachurus trachurus*): young fish survey, 1955–56. *Investl. Rep. Div. Fish. Un. S. Afr.* 29:1–36. Pretoria.

FROST, P. G. H., SHAUGHNESSY, P. D., SEMMELINK, A., SKETCH, M. & SIEGFRIED, W. R. (in press). The response of jackass penguins to killer whale vocalizations. *S. Afr. J. Sci.*

FROST, P. G. H., SIEGFRIED, W. R. & BURGER, A. E. (in press). Behavioural adaptations of the jackass penguin to a hot, arid environment. *J. Zool.*

FROST, P. G. H., SIEGFRIED, W. R. & COOPER, J. (in press). The conservation of the jackass penguin. *Biol. Cons.*

JACKSON, F., SIEGFRIED, W. R. & COOPER, J. (in press). A simulation model for the population dynamics of the jackass penguin. *Trans. R. Soc. S. Afr.*

KOOYMAN, G. L. 1975. Behaviour and physiology of diving. In, *The biology of penguins* (ed. B. Stonehouse). London: Macmillan.

MARCHAND, J. M. 1952. *Rep. Div. Fish. Un. S. Afr.* 22 for 1950.

MCLACHLAN, G. R. & LIVERSIDGE, R. 1970. *Roberts' birds of South Africa*, 3rd ed. Johannesburg: C.N.A.

POULTER, T. C. 1969. Sonar of penguins and fur seals. *Proc. Calif. Acad. Sci.* 36:363–380.

RAND, R. W. 1960. The biology of guano-producing sea birds: the distribution, abundance and feeding habits of the Cape penguin *Spheniscus demersus* off the south-western coast of the Cape Province. *Investl. Rep. Div. Fish. Un. S. Afr.* 41:1–28. Pretoria.

STONEHOUSE, B. 1967. The general biology and thermal balance of penguins. In, *Advances in ecological research* (ed. J. B. Cragg), 4:131–196. London: Academic Press.

WESTPHAL, A. & ROWAN, M. K. 1971. Some observations on the effects of oil pollution on the jackass penguin. *Ostrich* Suppl. 8:521–526.

WEVER, E. G., HERMAN, P. N., SIMMONS, J. A., & HERTZLER, D. R. 1969. Hearing in the blackfooted penguin, *Spheniscus demersus*, as represented by the cochlear potentials. *Proc. natn. Acad. Sci. U.S.A.* 63:676–680.

ZOUTENDYK, P. 1965. A convenient method for recording and processing field data. *Ostrich*, 36:12–14.