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THE BLACK-FOOTED PENGUIN *SPHENISCUS DEMERSUS* IN ARTISZOO AMSTERDAM, 1961-1982

by

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SUMMARY

Black-footed Penguins, *Spheniscus demersus*, have been living in an open air enclosure in Artiszoo since 1961. Their numbers varied from 7 to 103 in the period under study extending from 1961 to 1982. The information used in this survey is derived from records made by the zoo keepers and from a study of the behaviour of the penguins that was performed in 1979-1980.

The pair bond between breeding birds appears to be very strong, the only bird that ever disassociated itself returned to her first partner after one year. However, the penguins seem to find a new partner in a very short time if they happen to forfeit their first partner.

The couples have a strong tendency to breed each season in the same burrow. The occasional shifting to other burrows seems not to be related to the fate of the first clutch. The partners stayed together in nearly all cases in which breeding birds changed burrows. A burrow seems to get new owners only when the previous couple vacates it. This has had the consequence that, in some years, young couples could not install themselves because there was a lack of nesting places.

The clutch size is two and the number of clutches per season is one or two, three is less common. The birds are probably encouraged to lay a second or third clutch when the previous one fails visibly in an early stage. The frequency of laying second and third clutches might decrease if the penguins in Artiszoo were allowed to revert to their natural cycle of guarding their young for 80 days instead of the enforced period of only 42 days.

The breeding season runs from August to May and has two peak periods of egg-laying, one in August/September and one, less extreme, in December. The timing of breeding varied from year to year, in some years the first egg-production peak appeared in July/August and in others it appeared only in October.

The penguins in Artiszoo start breeding for the first time when they are two years or older, just like the penguins in South Africa.

Since 1965 the population growth has been caused entirely by the reproductive qualities of 19 birds and their descendants.

The hatching success of eggs decreased spectacularly in the years after 1971 when the number of available adults exceeded the figure 25, and since that time relatively more eggs disappeared or were found to be broken. This study shows that the decline of the hatching success is caused both by a lack of nesting places and the increase of the number of penguins living in the enclosure.

RÉSUMÉ

Les Manchots du Cap (*Spheniscus demersus*) vivent depuis 1961 dans un clos à l'air libre du zoo d'Amsterdam (Artis). De 1961 à 1982 leur nombre a varié de 7 à 103. L'information mise à profit pour le présent travail provient des observations réalisées par les gardiens du zoo dès 1961, ainsi que d'une étude du comportement de ces manchots, réalisée en 1979-1980.

Il y a un lien fort serré entre partenaires; le seul exemplaire qui s'était dissocié de son partenaire pendant cette période, est revenu à celui-ci après un an. Cependant, si par hasard les manchots ont perdu leur premier partenaire, ils semblent en trouver fort rapidement un autre.

Les couples ont une forte tendance à nicher toujours au même gîte; s'il y a passage à d'autres gîtes, ceci n'est pas conditionné par le sort de la première couvée. Dans presque tous les cas où il y a eu changement de gîte, les partenaires sont restés ensemble. Il semble qu'un gîte ne reçoit de nouveaux locataires que s'il a été abandonné par les anciens; par conséquent, il y a des années où des jeunes couples ne peuvent pas s'installer à cause du manque d'endroits propices à la nidification.

Il y a une ou deux couvées par saison, trois couvées étant une situation moins commune; il y a deux œufs par couvée. Les oiseaux sont probablement encouragés à passer à une deuxième ou troisième couvée quand il est visible que la première a échoué à un stade précoce. Une deuxième ou troisième couvée devient un phénomène moins fréquent si on permet aux manchots de revenir à leur cycle naturel (jeunes gardés par les parents pendant 80 jours, et non seulement pendant 42 jours comme dans les conditions imposées au zoo Artis).

La période de reproduction s'étend d'août à mai et il y a deux maxima de ponte, un premier en août-septembre, un second, moins important, en décembre. Mais le moment exact de la reproduction varie d'une année à l'autre, certaines années le maximum de la première ponte se situe en juillet-août, d'autres années en octobre seulement.

Dans le zoo d'Amsterdam, les manchots ont leur première période de reproduction alors qu'ils sont âgés de deux ans ou plus, exactement comme ceux d'Afrique du Sud.

Depuis 1965, ce sont les qualités reproductives de 19 exemplaires qui ont été responsables de l'augmentation des effectifs de la population.

Le succès de l'éclosion a enregistré une baisse spectaculaire après 1971, alors que le nombre d'adultes présents avait dépassé 25, et depuis la même époque le nombre d'œufs disparaissant ou étant trouvés brisés a augmenté. L'étude montre que ce déclin du succès de l'éclosion est provoqué d'une part par le manque d'endroits de nidification, d'autre part par l'augmentation du nombre des manchots vivant dans le clos.

INTRODUCTION

This study is one in a series from a research programme conducted under agreement between the University of Amsterdam and the Royal Zoological Society "Natura Artis Magistra", Amsterdam. One of the species under study is the Black-footed Penguin *Spheniscus demersus*. From May 1961 on, these penguins have been living in Artiszoo in an open air enclosure. Since that time they have bred regularly, by which the population has steadily increased to its present level. A summary of the breeding results up to 1977 is given by Dekker (1967) and Lensink & Dekker (1978). All penguins have been ringed adequately since 1978 and the flow of data about individually recognizable penguins that became available by means of this method is an important source of information used in this survey.

The present paper reports on site tenacity, pair bond, first breeding and the timing of breeding, it gives a description of the colony and its development, and it provides also possible explanations for the very noticeable decline of the hatching success of eggs in the years after 1971.

TERMINOLOGY

The terms: "colony" and "population" are used to describe the entire group of Black-footed Penguins, also named Jackass Penguin, living in Artiszoo. "Territory" is the area that a bird or pair defends against sonspecifics, and is usually the breeding hole and its direct surroundings. "Incubation stage" is the period from the time the first egg is laid until it hatches.

"Guard stage" is the period from the time that the first egg hatches until the chicks leave their parents, either because the zoo keepers take them from the nests or because they are old enough to take care of themselves. An "unsuccessful clutch" is a clutch of which no chicks are raised to an age of six weeks or older. A "successful clutch" is a clutch of which at least one chick achieves the age of six weeks. A "chick" is a young bird from the time of hatching until it leaves its parents. A "juvenile" is an immature bird which is in the juvenile plumage and is independent of its parents. An "adult" is a bird in adult plumage of about two years old or more.

I used two specific terms for displays: "Allopreening" is the behaviour in which birds preen each other, it can be both non-reciprocal or simultaneous. The "Arms Act" is the usual prelude to copulation; the male approaches the female in a specific posture and presses his breast against her back. He gently pats her sides with his flippers and attempts to push her in the sitting position. A more comprehensive description of both displays can be found in Eggleton & Siegfried (1979).

MATERIALS

Accommodation

In order to create a facsimile environment to the natural habitat of penguins, a new open air enclosure was constructed in the shade of the aquarium building at Artiszoo. It was put into use in May 1961.

The entire enclosure measures 880 m² of which 625 m² is allotted to a sandy shore backed by rocks and the remaining 255 m² given over to

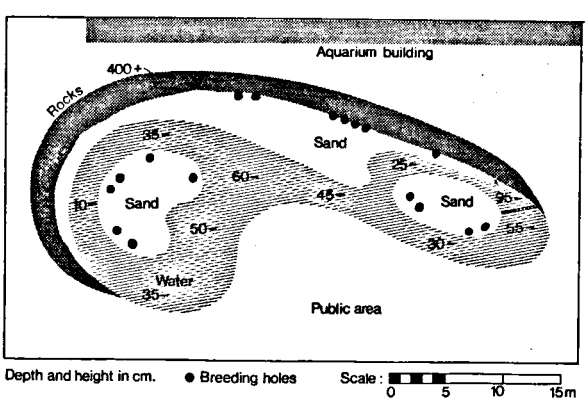

Fig. 1. Ground plan of accommodation for Black-footed Penguins at Artiszoo (after Lensink & Dekker, 1978).

Fig. 2. Burrows situated on one of the islands at Artiszoo.

water. The rocks are situated on the south side of the compound and vary in size from 4 to 5 m. These rocks provide the background to a pool in the shape of a figure eight within which are two islands (fig. 1). The pool varies in depth from 0 to 95 cm and it is filled with tap-water. More information on the accommodation is contained in Lensink & Dekker (1978).

The rocks and islands are provided with breeding holes or burrows as they are termed, which are constructed from bricks with a sand floor and have a depth of 60 cm with the entrance approximately 45 cm high and 30 cm wide (fig. 2). The number of burrows tends to vary according to the number constructed by the zoo keepers when deemed necessary and the number of bad holes that are demolished. At the end of 1979 there were 21 burrows. Seven of these holes were situated with the rear in the rock and the remaining fourteen were erected on the surface of the islands.

Number of birds

The number of Black-footed Penguins living in this enclosure varied from 7 to 103 in the period from 1961 to 1982. In October 1979 there were 62 adults, 28 juveniles and 2 chicks in Artiszoo.

The presence of other species, viz. penguins and other birds (Dekker, 1967; Lensink & Dekker, 1978) did not seem to influence the breeding results of the Black-footed Penguins and is therefore not considered in this paper. An exception is the colony of Humboldt's Penguins *Spheniscus humboldti* that lived in Artiszoo until 1974. This species was removed mainly because it was thought there might be some competition between them and the Black-footed Penguins, especially in selecting breeding accommodation (Lensink & Dekker, 1978).

Treatment and care of the penguins

The colony is fed with fish twice a day at 9.00 a.m. and 3.30 p.m. All penguins are trained to eat from

the hand of the keeper. The breeding penguins are fed on their nests.

From the age of six weeks the chicks are isolated from their parents in order to train them to eat from the hand of the keeper. With the many free-flying birds such as gulls and Grey Herons, which prove to be formidable rivals at feeding time, it is essential to ensure that each penguin receives its correct ration of food and this method of feeding has been adopted as the simplest solution. The young are usually accustomed to hand feeding after 4 to 8 weeks and are then permitted to return to the colony, ringed with a serial number fixed to their tarsus or to their wing.

The keepers empty and clean burrows on the same day as they take the six week old young from the nests or when it is clear that the clutch or brood was a failure.

In the breeding season, the keepers place bunches of nesting material comprising of coarse and well-dried twigs of *Potentilla aborescens* on several places in the enclosure. The supply is replenished when necessary.

METHODS

The conclusions given in this study are mainly based on reports made by keepers of Artiszoo. The information from these reports is supplemented with data from the observations that were made in 1979/1980 during a study of the behaviour of the penguins.

History

Records regarding Black-footed Penguins at Artiszoo first appeared in April 1956; the responsibility for the reports rested with the keepers. I have used all the data from 1 May 1961 to 12 May 1982 that involve population growth and breeding results.

It is indeed unfortunate that the available information concerning this species is very limited in the first years. But the records improved as time passed and the population grew. From 1970 on the birds were ringed and for that reason individually recognizable. In 1976, the keepers began to record the parents' ringnumbers when the young were taken from their nests. The reports have become more informative since that time. However, the material of the rings proved to be too weak and rings either disappeared or the inscription was erased through wear and tear and much information was irretrievably lost. Not until 1978 did all birds receive new, stronger rings and almost all the available information regarding individual penguins was gathered during the last four years of research.

Study of behaviour

The penguins were observed from October 1979 until February 1980 and during the first week of March 1980. Our surveillance was made between 10.00 a.m. and 3.30 p.m. for about two hours a day.

We witnessed the behaviour of 74 adult penguins on land. Special attention was given to interactions and activities that were linked somehow with breeding behaviour, e.g.: agressive displays, allopreening, copulatory behaviour, copulation and nest-building activities.

All observations were noted and the time was recorded every five minutes. We endeavoured to obtain complete descriptions of the different displays, supplementing our studies with the aid of both still and cine photography.

Identification

A very sizeable proportion of the penguins, 92 out of 95, were ringed and the ringnumbers could be read with the aid of binoculars.

The penguins differ not only in ringnumber but also in the black-and-white patterns on the beak, feet and the underside of their flippers. In addition, they all have a different pattern of black spots on their white underside and throat (fig. 3), each spot being formed by a single feather with a black tip and a much lighter base. The patterns formed by the black spots return after moulting.

In order to identify the individual penguins, we read the ringnumber and made a drawing from the pattern of the black spots on the belly and throat of each bird (Leloup, unpubl.). After a while we recognized most of the birds by the pattern of spots.

Fig. 3. Black-footed Penguins can be individually recognized by the different patterns of black spots on their white underside.

The birds are sexed by the keeper at the time he isolates the six-week old young from the nests: he notes the ringnumbers of both breeding birds and designates the bigger one the male and the smaller the female. However, where possible, observations of copulations were used for sexing as well. Eleven breeding couples were sexed, independently, by both methods and this led to the same results in all cases.

RESULTS

Site tenacity and pair bond

In the period from July 1976 to May 1982 the keepers reported 267 clutches, 88 of which could not be used in this part of the study because either the parentage of the eggs was unknown or the eggs belonged to a breeding couple that, according to the reports, bred only once. The remaining 179 clutches belonged to 35 different breeding birds and their mates. In 17 of the remainder only one of the partners was known; both partners were known in all other cases.

Table I indicates that 18 of the 35 breeding birds never changed burrows, 11 birds changed once and 6 other penguins shifted more than once. At least one change of burrow was enforced because the old burrow was demolished. It occurred twice that a breeding couple changed burrows,

TABLE I

Numbers of burrow and partner changes of individual birds.

N of breeding birds	*N* of shiftings	*N* of partner changes	Total number of clutches produced by these birds
18	0	0	90
11	1	0	47
2	2	0	11
2	3	0	19
1	3	2	7
1	4	1	5
35	28	3	179

produced one clutch in the new burrow and returned to the former burrow again. One couple deserted the eggs and the other couple raised a young from their eggs in the new burrow.

Table I also shows that only 2 of the 35 breeding birds changed mates, and this indicates that there is a strong bond between paired birds.

One female had a change of mate after her first partner died (her age at that time: 5 years and 10 months). She had five clutches, all unsuccessful: two with her first mate and three with her second mate. She laid every clutch in a different burrow. After she was sold in 1981 her partner stayed in the last burrow and found himself a new mate (her age: 2 years and 5 months, his age at that time: 3 years and 10 months). This new couple has had two clutches up to now: one successful and one unsuccessful. (This case of partner change is not shown in table I.)

The other bird changed her mate after a successful clutch with her first partner, leaving him and his burrow next season and having two clutches, one successful and one unsuccessful, with another male in another burrow. In between those clutches she was twice seen performing the Arms Act (fig. 4), this is the usual prelude to copulation (Eggleton & Siegfried, 1979), with her first partner in his territory. This is the only case in which we saw this display performed by birds that did not form a pair. After that season of "unfaithfulness" she went back to her first partner and his burrow and since that time they have had four clutches, two successful and two unsuccessful. During his lonely season the male was reported several times in a breeding posture in his empty burrow. For a while it seemed that he was interested in another penguin; he followed her sometimes and he allowed her to walk in his territory but he chased her away when his first female approached his burrow. The other male that was left alone by this female stayed in his burrow and found another mate. He has had two successful clutches with her to date.

It must be noted here that in both cases the males stayed in the same burrow after the change of mate and that the two females changed burrows together with the change of mate.

Another indication for a strong pair bond is the fact that in 22 of 28 cases of shifting the couples stayed together. In three cases it is unknown if partners stayed together after shifting. The other three cases have been described above.

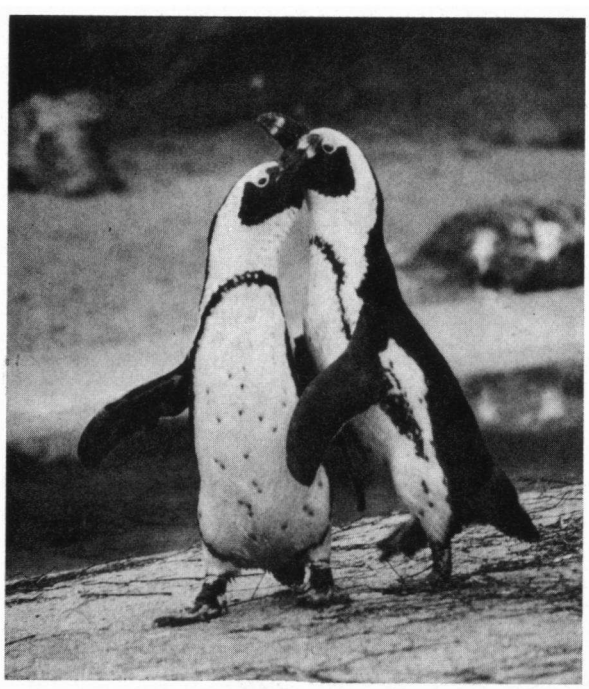

Fig. 4. Two adults performing the Arms Act.

TABLE II

Change of burrow without change of mate.

	Burrow		
	Same	Shifted	% Shift
Same season	71	8	10
Next season *	44	17	28

* When a pair produced more than one clutch in a season, it was the final nesting burrow of the previous season and the first one of the following season that was counted.

Table II illustrates that burrows were changed in only 10% of 79 cases in which pairs laid two or more clutches in one season. The same burrow was used from one season to the next in 72% of the cases.

At least two species of penguins, *Eudyptula minor* and *Megadyptes antipodes*, are more liable to shift to a different burrow after breeding unsuccessfully (Reilly & Cullen, 1981; Richdale, 1957). However, as illustrated in table III, there is no evidence to indicate that this is also true for

the Black-footed Penguins in Artiszoo. There is only a slight distinction in the percentages of shifts after successful and unsuccessful clutches; within a season, 8% and 13% and from one season to the next 28% and 29%, respectively.

TABLE III

Change of burrow following breeding success or failure without change of mate.

Next clutch	Fate of previous clutch	Burrows used for next clutch		
		Same	Shifted	% Shift
Same season	S	36	3	8
	U	35	5	13
Next season	S	21	8	28
	U	23	9	29

S = successful, at least one chick achieved the age of six weeks; U = unsuccessful, no chicks raised to an age of six weeks or older.

The data relating to penguins in Artiszoo do not confirm the theory that young, inexperienced breeding birds are more liable to shift to a different burrow than birds that have already produced several clutches (Richdale, 1957). Ten penguins in Artiszoo have had a clutch before the age of three. Five of them, four males and one female, belong to the group of 18 penguins that did never change burrows. The remaining five, also four males and one female, belong to the group of 17 penguins that shifted at least once. Two specimens shifted within their first breeding season, the other three birds changed burrows from their first breeding season to the next.

During our study of the behaviour of the penguins we noticed that there was a lack of burrows. This situation could force some breeding couples to breed in burrows that in their view are of poor quality. As a consequence they will change burrows as soon as possible. The data in the reports show that most burrows get new owners only when they are vacant. In 8 out of 40 cases the burrow was newly built. In at least 20 cases the burrow was empty because the previous occupiers were sold or had shifted to another burrow or because one of the partners had died. In the remaining 12 cases there is no evidence indicating whether the burrow was empty or not when the new owners seized it.

Clutch size

The Black-footed Penguins in Artiszoo laid two eggs in each clutch in 84% of 478 cases. In 15% of the cases the keepers reported only one egg; possibly an egg had been lost between successive checks. There were only five clutches (1%) of three eggs. In at least three cases those eggs belonged to two females and one male.

Second eggs are laid usually 1 to 6 days after the first (mean = 4, N = 258), the incubation period averages 38 days (Lensink & Dekker, 1978) and the eggs hatch usually with an interlude of 1 to 6 days (mean = 3, N = 81).

Number of clutches per season

Table IV indicates that the breeding couples lay one or two clutches per season, three clutches is

TABLE IV

Approximations of the number of clutches laid by breeding couples per season.

N of clutches per season	N of burrows *	% of burrows	% of "one egg" cases **	N of pairs ***	% of pairs
one	69	28	29	41	40
two	124	50	13	45	44
three	49	20	49	17	16
four	4	2	100	0	0

* The number of cases in which a burrow contained one, two, three or four clutches in a season over the period from 1 July 1966 to 12 May 1982.

** The percentage of cases in which at least one clutch consisted of only one egg.

*** The number of cases in which a pair of penguins had one, two, three or four clutches per season. This information originates from 35 different pairs over six years (1976—1981).

less common. In 11 of 17 cases in which a pair had three clutches, all three clutches were unsuccessful. In 2 of 17 cases the first two clutches each gave birth to at least one chick that achieved the age of six weeks. It was never recorded that all three clutches were successful, at least one was unsuccessful in all cases.

The data in table IV should be examined with some caution because the number of clutches laid in one season in one burrow might have been the product of different breeding couples. But as a consequence of the site tenacity of the couples, as described previously, conclusions can still be drawn. The right hand section of table IV demonstrates the number of cases in which it was certain that the clutches belonged to one pair. But there is always a possibility that some of the couples produced more clutches than was otherwise reported because there were some clutches of which the parentage was unknown.

TABLE V

Frequency of laying a second clutch in relation to the fate of the first clutch. This information originates from 35 different pairs over six years (1976—1981). The cases in which a third clutch was laid have been eliminated.

Fate of first clutch	Second clutch		
	Not laid	Laid	% re-laying
S	26	35	57
H	5	9	64
F	10	18	64

S = successful, at least one chick achieved the age of six weeks; H = hatching success, at least one egg hatched but the chick(s) died before the age of six weeks; F = failure, no eggs hatched.

Table V shows that when the first clutch was successful, a second clutch was laid in 57 percent of the cases. When the first clutch or brood was lost, a second clutch was laid in about 64 percent of nests, irrespective of whether eggs or chicks were lost.

Date of laying

Fig. 5 illustrates the number of eggs laid in each month over the years 1966 to 1982 and the percentages of these eggs that hatched. The period from July 1975 to June 1976 has been eliminated

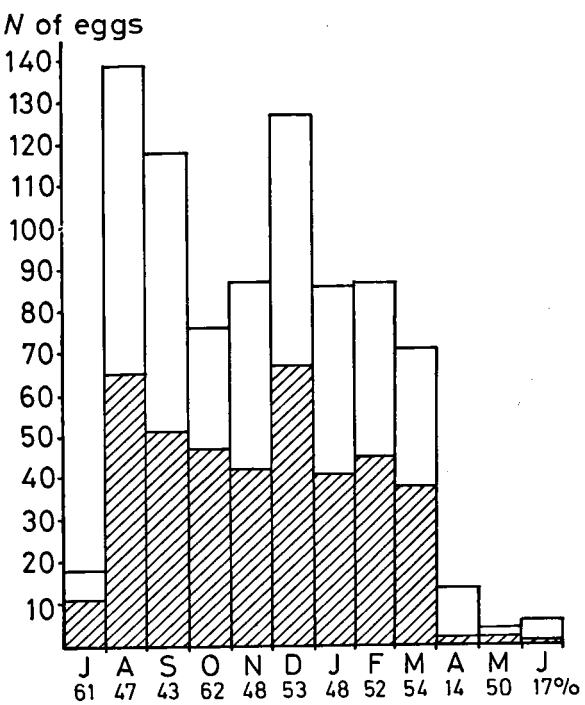

Fig. 5. Number of eggs laid and number of eggs hatched (shaded part) in each month of the period 1966—1982 and the corresponding hatching percentages.

because in this period almost half of the population died as a consequence of an aspergillosis outbreak. The period from 1961 to 1966 has been omitted because there is no information available concerning this period that could have been used in this figure. The influence of these data cannot have been of great importance to the general outline of the figure anyway because of the small number of eggs that had been laid during this period (total number was 27).

Eggs have been laid in every month of the year, but to date no eggs have been recorded between 15 June and 15 July. The breeding season for the Black-footed Penguins in Artiszoo runs from August to May [1]. The production of eggs reaches a peak in August and September and there is a second peak in December. The hatching success is approximately constant for eggs laid during the period from August to March (the hatching percentages varying from 43% to 54%), with the

[1] Because the breeding season overlaps the end of the calendar year, for brevity and convenience I refer to a season by the year in which it started, e.g. 1961 for 1961-1962.

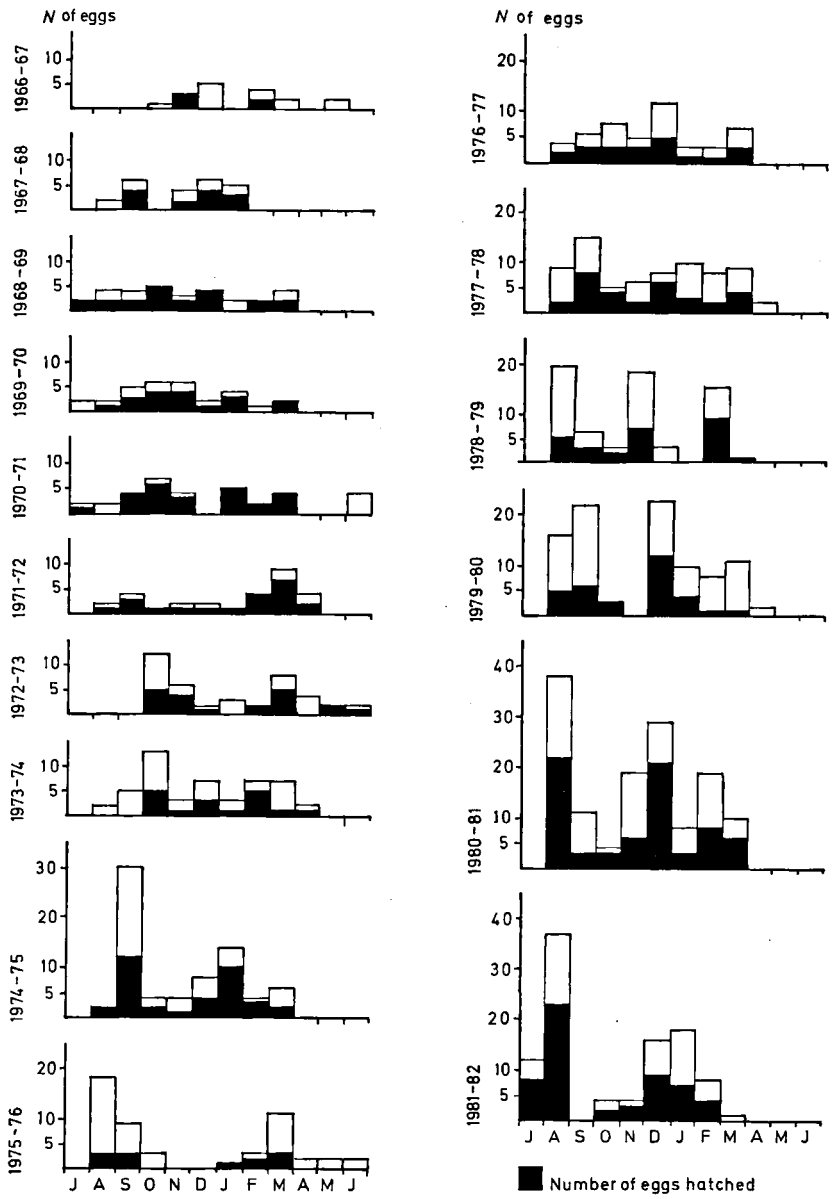

Fig. 6. Number of eggs laid in each month over the period 1966—1982.

exception of October in which the hatching percentage reaches a maximum of 62%. The hatching success is very small in the months after the most productive period.

The breeding season varies considerably from year to year, but there is no indication that it shifted in one particular direction during the last 15 years (fig. 6).

The histogram of the season 1975 needs some special attention; the penguins were taken from the enclosure on 15 October 1975 because of an aspergillosis epidemic that killed 49 penguins whereby nearly all eggs laid were lost before they hatched. The surviving birds, numbering about 38, returned to the enclosure on 15 December 1975 and it is interesting to note that the number of eggs laid in the period from January to June 1976 is not different from the quantity laid with a number of adults (34) pro rata in the season 1972. This might indicate that the penguins, which

have a strong bond with their partner as shown previously, find another mate on a very short term basis if they should happen to forfeit their first partner. The hatching percentage of eggs was lower than in other years but this could be caused by the probably delicate condition of the birds, or because the eggs were laid late in the season, or perhaps because the new breeding partners were not yet accustomed to each other.

Age at first breeding

Table VI shows that all penguins older than four years had at least one clutch before May 1982. Four of ten penguins aged between 2½-3½ years had at least one clutch. The same applies for just one of seven penguins aged between 1½-2½ years old, his age was 2 years and 4 months at that time. In addition, five young breeding couples were recorded in January 1982, which wanted to build nests but were unable to find suitable places. This same situation was discovered during our study of behaviour in 1979: three young couples were building nests in the open sand. These attempts could not succeed because the keepers dismantled the nests every day. The keepers had experienced that clutches in open nests are doomed to fail because of too much rainfall and therefore they destroyed the nests. The birds that were not allowed to build nests produced their first clutch only in the following year, when there were more burrows available. The fact that they did not have a clutch in 1979 is an indication that penguins do not lay eggs when they have not built a proper nest even if they are physically capable of breeding.

TABLE VI

Breeding status of birds of known age in May 1982.

Age in years	N of birds having started breeding ♀	♂	N of birds not yet breeding	n	Proportion of birds that have started breeding
4—9	7	13	0	20	1.0
3—4	3	1	6	10	0.4
2—3		1	6	7	0.2
1—2			8	8	0
0—1			22	22	0
Total	10	15	42	67	

The ages of eight out of ten females on the day that their first eggs were reported varied from 2 years and 5 months to 4 years and 3 months (mean = 3 years and 2 months). Two females, both born in 1973, achieved ages of 6 years and 8 months and 6 years and 11 months before they had their first clutch. In addition, at Baltimore Zoo where there was a problem of surplus of males, the mean age of sexual maturity (also evidenced by the laying of the first eggs) of Baltimore bred females was 2 years and 5 months (range: 2 years and 2 months — 2 years and 10 months) (Gailey-Phipps, 1978). In the 15 males of table VI these ages vary from 2 years and 2 months to 3 years and 7 months (mean = 2 years and 9 months). However, there is always a possibility that the penguins had a clutch in an earlier stage because there are clutches of which the parentage is unknown. This information suggests that in Artiszoo females have their first clutch at a later age than males, but table VII demonstrates that there has been a lack of adult males in the seasons 1978 and 1979. This condition was neutralized in 1980 because 80% of the birds born in 1976 and 1977 happened to be males. There is regrettably no information available about the proportion of males and females in the previous seasons.

TABLE VII

Sex ratio in adults.

Season	♂♂	♀♀	Sex unknown
1978	20	27	4
1979	26	30	6
1980	30	29	6

As a consequence of the lack of males, pairs were formed in which the female was much older than the male; in four out of nine couples of known ages the female was more than 18 months older than her partner. There is only one case in which the male was much older than his female (17 months). The difference in ages between the partners of the remaining four couples was less than 6 months.

During the observation of the behaviour of the penguins in 1979 we discovered that two out of

twelve birds with ages between 1½ and 2½ years old performed a complete breeding behaviour: they had formed a stable association with one other penguin, they copulated and they built nests. Both birds were 2 years and 2 months old at that time. Three of these twelve birds performed an incomplete breeding behaviour: they were not associated to one particular other bird but they followed some other birds repeatedly and they were seen allopreening them (fig. 7). The remaining seven birds were never recorded as performing such behaviour. None of 16 birds with ages between ½ and 1½ year old showed the complete breeding behaviour as described above. Seven of them performed the incomplete breeding behaviour and the remaining nine birds did not show any of these interactions.

The development of the colony of Black-footed Penguins in 21 years

Table VIII gives a summary of the available data on the development of the colony.

Six of the twelve penguins introduced into the new enclosure in May 1961 had already lived in the zoo for 10 to 14 years. In the period 1961 to 1965 five penguins died that had been in the zoo for periods varying from 12 to 18 years. These are respectable ages according to Jackson et al. (1976); they reported that captive Jackass Penguins rarely live longer than 15 years.

April 1965 was the very last time that penguins were bought, and since then the growth of the colony has been dependent upon the reproductive qualities of 19 birds and their descendants.

The number of birds breeding in Artiszoo varied from year to year. The reports did not mention how many penguins were actually breeding in any season. An indication for this quantity is the number of nesting places in which eggs were laid. It is only an indication because some couples shifted from one breeding hole to another within the same season.

Approximations of the numbers of birds that would have bred if all conditions had been opti-

TABLE VIII

Development of the colony of Black-footed Penguins *Spheniscus demersus* in Artiszoo, Amsterdam.

Season *	*N* of penguins	*N* of adults	*N* of occupied nesting places	*N* of eggs laid	*N* of eggs hatched	*N* of 6 week old chicks	Mortality of penguins older than 6 weeks	Birds bought (b) sold (s)
1961	12	12	?	0			1	
1962	11	11	?	2	0		4	
1963	7	7	?	8	4	4	0	
1964	11	7	?	7	2	1	3	10 (b)
1965	19	11-14	?	10	5	5	2	
1966	22	16	5	17	5	2	5	
1967	19	12	7	23	13	9	1	
1968	27	16	7	30	21	17	0	13 (s)
1969	31	18	9	30	18	13	2	
1970	42	25	9	34	25	20	5	
1971	57	24	9	29	20	16	3	
1972	70	34	14	41	20	18	1	4 (s)
1973	83	51	13	49	19	15	2	13 (s)
1974	83	50	19	72	36	22	2	
1975	103	66	17	51	12	8	49	10 (s)
1976	52	32-44	16	48	21	16	3	
1977	65	41	20	72	31	12	0	
1978	77	51	17	65	27	16	3	
1979	90	62	27	93	33	20	4	21 (s)
1980	85	65	29	138	72	30	5	29 (s)
1981	81	63	28	100	56	49	5	26 (s)

* The number of penguins and of adults designated in the second and third column indicates the number at the beginning of each season.

Fig. 7. Simultaneous allopreening of two adults.

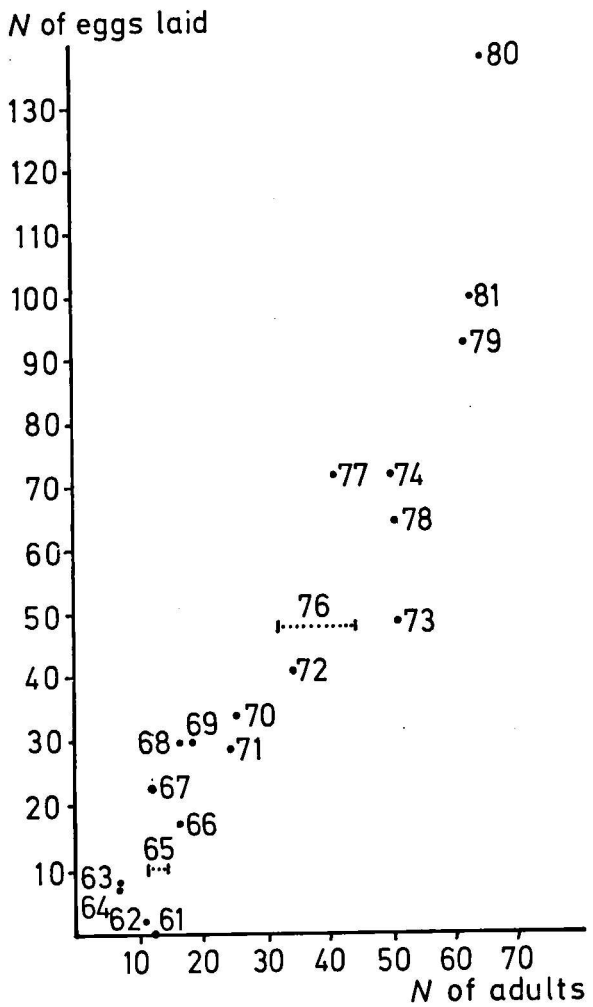

Fig. 8. The relationship between the number of adults and the number of eggs laid. The index numbers given in figs. 8-11 indicate from which season the information is derived, e.g. 61 for the season starting in 1961.

mum are given by the numbers of penguins older than two years, alive in the enclosure at the beginning of each season. Unfortunately, the exact numbers of available burrows are unknown. So, in the following sections comparisons are made with the total number of adults present in the enclosure.

The penguins that were sold were mainly young birds which took no part in breeding, exceptions are six adults sold in May 1980 and 11 adults sold in May 1981.

In the autumn of 1975 almost half of the colony died because of an aspergillosis outbreak (Lensink & Dekker, 1978) and this season will therefore not be used in the analysis of the development. It is not recorded how many of the victims were adult birds, therefore it is impossible to give the exact number of adults in the season 1976.

The mortality rate in other years is much lower and varies from 0 to 5 birds that were older than 6 weeks.

The number of eggs produced in any season increases with the number of adult penguins living in the enclosure at the beginning of the season (fig. 8). This was only partly caused by the fact that with the greater number of adults available to produce, it naturally follows that more eggs will be laid. Another reason, which was of primary importance in the seasons 1972 to 1979, is that the percentage of eggs that failed visibly in an early stage, increased with the growth of the number of adults and that the breeding couples were thereby induced to lay second and third clutches (see below).

Fig. 9 illustrates that, in accordance with expectations, before 1972 the number of eggs that hatched increased with the number of available adults. However, from 1972 to 1979 this increase was relatively insignificant when the number of adults grew from 25 to 62. This suggests that there is a limit to the number of eggs that can hatch, which is determined by the number of adults present. After 1979 the number of hatched eggs increased spectacularly when the number of adults rose further to 65. This indicates that it was not only the number of available adults that determined the number of eggs that hatched, but that other factors possibly influenced this number as well. This will be examined in a later section.

Fig. 10 shows a similar picture, but this graph indicates the relationship between the number of chicks that attained the age of six weeks and the number of available adults. It can be seen that there was no increase at all in the number of six-week old young when the adult population grew from 25 to 62, but the increase was remarkable when the number of adults grew further from 62 to 63 and 65.

The number of chicks that attain the age of six weeks is thought to be strongly related to the influence of living in captivity. For that reason my conclusions in this study are based mainly on the numbers of eggs that hatched and not on the numbers of chicks that reached the age of six weeks. There are for example, strong reasons to believe that the death of many chicks in the breeding seasons 1977 and 1980 was caused by the quality of the fish they were fed with.

Fig. 11 demonstrates for each season the percentage of eggs that hatched compared with the number of adults living in Artiszoo at the onset of the season. I did not use the data of the years before 1967 because the number of pairs that laid eggs was very small: five or less. From 1967 on this figure was always greater than six.

Fig. 11 shows that there is a strong deviation between the hatching percentage of eggs before and after June 1972. From 1967 to 1972 the percentage of eggs that hatched was always more than 56% with a number of adult penguins below 25. In the following period from July 1972 to June 1980 the percentage of eggs that hatched decreased from 48% to 35% with a growth of adults from 34 to 62. However, in 1974 the hatching success was abnormally high, 50%, in comparison to the preceding and following

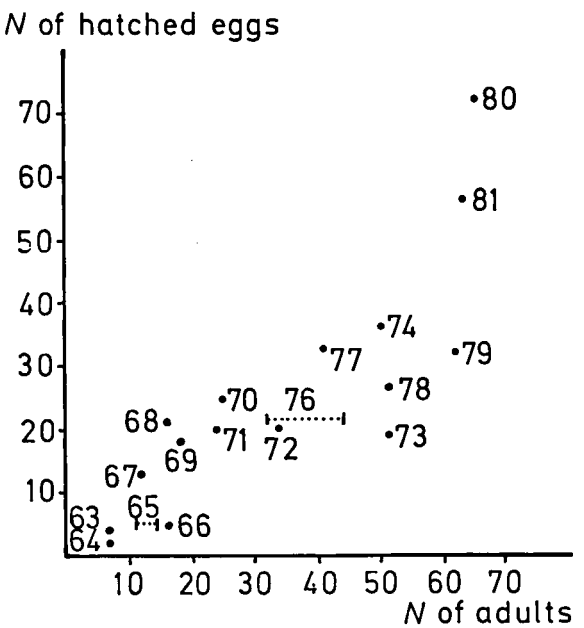

Fig. 9. The relationship between the number of adults and the number of eggs that hatched. For further explanation see fig. 8.

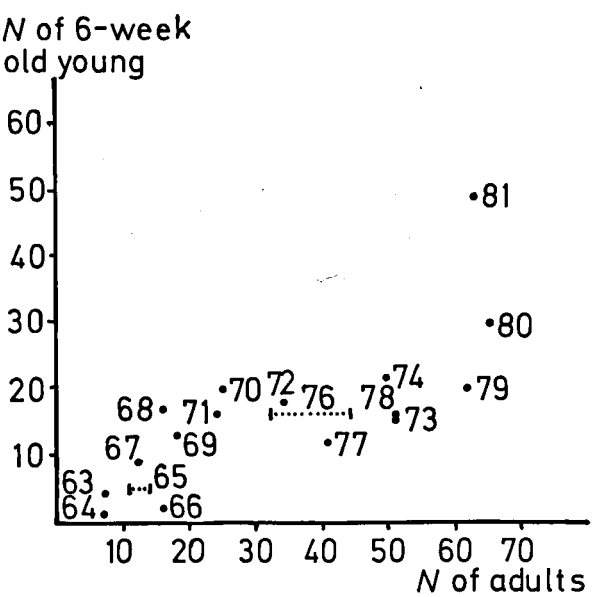

Fig. 10. The relationship between the number of adults and the number of young that attained the age of six weeks. For further explanation see fig. 8.

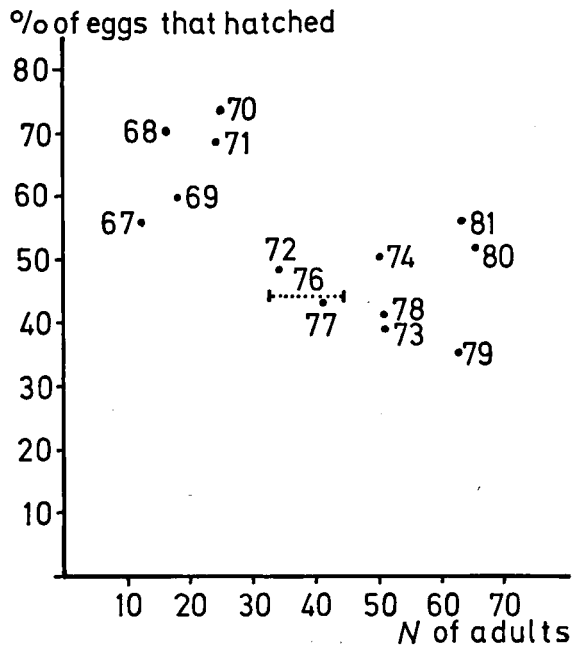

Fig. 11. The relationship between the number of adults and the percentage of eggs that hatched. For further explanation see fig. 8.

seasons. In the period from July 1980 to May 1982 the percentage of eggs that hatched is exceptional in spite of the abundance of adult penguins but it is still lower than the mean percentage scored when there were only 25 or less adults.

Table IX presents a summary of the available data on the fate of eggs during the periods 1967—1971 and 1972—1979. During the seasons 1980 and 1981, numerous alterations were made affecting the habitat of the colony and I consider it pertinent to delete them from this analysis; however, the figures are included in table IX. The table shows immediately that it is impossible to find the direct causes of failure by means of these data: of the eggs that were reported as lost, broken or overdue, it cannot be stated if they were fertilized or not. The eggs that are indexed with a question mark were only reported when they were laid, it is unknown what happened to them afterwards.

It is not only the difference in the number of eggs that hatched in each period that is statistically significant ($\chi^2 = 25.2$, $\alpha = 0.05$) but also the number of chicks that reached the age of six weeks is significantly higher in the first period than in the second ($\chi^2 = 5.2$, $\alpha = 0.05$), 77.3% and 64%, respectively.

Out of the chicks that died at an early age, 97% did so before they were three weeks old. When eliminating the season 1977 (the death of a lot of chicks in this season was presumably caused by feeding with the wrong fish) still 31% of the chicks died at an early stage but the difference between both periods is no longer significant ($\chi^2 = 2.3$, $\alpha = 0.05$).

The greatest differences between both periods are found in the percentages of eggs that disappeared, respectively 6.8% and 10.9%, and the percentages of eggs that were found to be broken, respectively 2.1% and 9.5%. The number of eggs that were lost by these causes is significantly higher after June 1972 than in the period preceding it ($\chi^2 = 17.2$, $\alpha = 0.05$). There is only a minute difference between the two periods in the percentages of eggs that were sterile, viz. 18.5% and 18.9%, respectively.

TABLE IX

Fate of eggs laid in the periods 1967—1971 and 1972—1979 and the seasons 1980 and 1981. N = number of eggs laid; n = number of eggs that hatched.

Season	N	percentage of eggs							% of young that died	n
		lost	broken	sterile	embryo died	?	overdue	hatched		
1967—1971	146	6.8	2.1	18.5	0.7	2.7	2.7	66.4	22.7	97
1972—1979 *	440	10.9	9.5	18.9	3.6	12.7	1.6	42.5	36.0	186
1980	138	10.1	8	16.7	9.4	3.6		52.5	58.3	72
1981	100	1	3	17	12	11		56	12.5	56

* Season 1975 omitted.

The eggs of which nothing more was known other than that they were laid were omitted from analyses. I can only conclude from the information available to date, that these eggs disappeared or were smashed and therefore perhaps were not included in the recorded data held by the zoo. If this conclusion is correct the already significant difference in the number of eggs that disappeared or were broken increases between the periods.

POSSIBLE EXPLANATIONS FOR THE LOSS OF EGGS

Predation

Throughout our observation period we never saw attempts by other birds to steal eggs or chicks from the nests. Our observations were made in daylight only, so regrettably we have no knowledge of what happened during the course of darkness. But it is a known fact that Great Skuas and Great Black-backed Gulls are very capable predators (Berry, Seely & Fryer, 1974; Cooper, 1974) and one or two specimens of both species have been always present in the enclosure.

Hatching success of young, inexperienced birds

The mean hatching percentage of eggs produced by 12 breeding pairs of which at least one bird was inexperienced and younger than three years old, is 43%. In only two of these couples both partners were younger than three years old, and none of their eggs hatched. This information originates from the period 1979—1981, the mean hatching percentage of eggs laid by the remaining couples in this period was 49%. This indicates that the possible negative influence of inexperienced, young birds on the hatching success of their eggs is only small or somewhat neutralized when they are aided by an older partner.

Time of isolation of the young

A difference in care-taking of the penguins before and after 1972 was found in the time of isolating the young from their parents. Until July 1969 the chicks were taken from the nests, or the enclosure, to learn to eat from the hand when they reached the age of 10 weeks or even more. In 1970 and 1971 this was reduced from 10 to 6 weeks and it has stayed so to date. This acceleration of the isolation of the chicks might have a negative influence on the breeding success of the population. It might be possible that the breeding birds get annoyed when their young are taken from the nests at ages of only 6 weeks old and that the parents disturb other nests while searching for their young. Here it must be stated that it was recorded several times that chicks younger than 6 weeks old had moved from the burrow in which they were hatched into another. However, we did not find any evidence to confirm this supposition during our study of their behaviour in 1979.

Another possibility is that the isolation of the young from their parents at ages in between 6-10 weeks old has a negative influence on the future breeding results of these chicks. The idea behind this statement is that the chicks of 6-10 weeks old are in a critical period in which they are receptive to learning processes related to breeding behaviour. That the penguins are more receptive to certain learning processes at this age than a few weeks later is indicated by the motivation of the keepers to accelerate the isolation of chicks, because it is easier to teach the birds to eat from the hand when they are about six weeks old than after this age. However, this supposition does not agree with the high hatching percentages of eggs in the seasons 1980 and 1981, and is therefore rejected.

Breeding results in new burrows

Table X shows the percentages of eggs that hatched in the "new" burrows, these were used only after June 1972 and also in the "old" burrows which were used since 1966, over the periods 1966—1971 and 1972—1979. The hatching percentage of eggs after 1972 is about the same for the "new" and the "old" burrows. The hatching

TABLE X

The percentages of eggs that hatched in the "old" burrows and in the "new" burrows in the periods 1966—1971 and 1972—1979.

	1966—1971	1972—1979 *
"Old" burrows	60.7%	44.1%
"New" burrows		42.4%

* season 1975 omitted.

success in the "old" burrows was 16.6% higher before July 1972 than afterwards. This implies that the decrease in breeding success is not due solely to bad results in new burrows.

Breeding results per burrow

The mean hatching percentages of eggs laid in each burrow vary from 23% to 75%; in each of the 17 burrows examined at least 20 eggs were laid over a period of 10 years. These differences might be caused by the construction and/or place of the burrow. But regarding the fact that I used information of only ten subsequent years and that the penguins, which can reach an age of about 15 years, have a tendency to breed in the same burrow year after year, these variations might as well be caused by differences in individual breeding qualities of the breeding birds. In addition, the construction is about equal for all burrows and the dimensions are almost the same as those of the burrows used by the Black-footed Penguins on Dassen Island, South Africa (table XI). The only difference is the height of the entrance, 45 cm in Artiszoo and 18 cm on Dassen Island. So there is no reason to assume that poor breeding results in Artiszoo are caused by the construction of the burrows.

TABLE XI

The dimensions of burrows on Dassen Island (based on data presented by Frost, Siegfried & Burger, 1976) and in Artiszoo.

Mean dimension (± SD) of 10 Jackass Penguin burrows on Dassen Island		Estimations of the mean dimensions of the burrows in Artiszoo
Depth	56.2 ± 14.8 cm	60 cm
Height at entrance	18.2 ± 1.8 cm	45 cm
Width at entrance	32.6 ± 4.5 cm	30 cm
Angle from horizontal	—27 ± 5°	0°

Lack of burrows

In the seasons before 1972 the number of adults increased from 12 to 25. With this increase more eggs were laid and the hatching percentage of the eggs increased likewise. Presumably there were enough burrows available for this group of adults.

After July 1972 the number of adults was higher than 25 and the hatching rate was much lower than in preceding years. A lack of breeding holes is a possible explanation for this phenomenon.

In the season 1973 only a small quantity of eggs was laid in comparison to the number of adults (fig. 8). In 1974 the 19 Humboldt's Penguins *Spheniscus humboldti* were sold because it was thought that there was competition between them and the Black-footed Penguins, especially in selecting breeding accommodation. This colony of Humboldt's Penguins had lived in the enclosure since 1961, and until 1974 they had hatched 54 young. In the next season the Black-footed Penguins laid 23 eggs more than the previous year while the number of adults remained the same (51 and 50). The hatching percentage of the eggs also increased from 38.8% to 50%.

Something similar happened in 1979/1980. In the season 1979 the penguins rehabilitated 6 burrows that had not been used during the foregoing season. Two of them had not been used for three subsequent seasons. I suppose that in comparison, these burrows were less attractive for the breeding couples than the other ones. Three couples created their nesting places in the open air on the surface of the rocks. Four other couples attempted to build nests in the sand, but these were all removed by the keepers, with the exception of one. It seemed to be apparent that there was a lack of burrows in the season 1979. The number of adults in July 1979 was 62. In September 1980 at least 8 new burrows became available. In 1980 and 1981 the number of adults was 65 and 63 respectively, and the percentage of eggs that hatched increased from 35% in 1979 to 53% in 1980 and to 56% in 1981. The number of occupied nesting places in 1979 (27) was not much different from the quantity used in 1980 and 1981 (29 and 28 respectively), but the quality of some nesting places was much lower in 1979, e.g. the four nests in the open air.

The increasing number of penguins living in the enclosure

We observed several occasions in which the birds were frightened by the unexpected visit of a keeper. Their reaction was to flee into the nearest

Fig. 12. Penguin in burrow on the right adopts a pose designed to threaten the penguin that has approached too near.

burrows, even if these were occupied. It is very likely that they caused damage and destruction to the eggs or chicks through the ensuing fights which tend to erupt as a result of the intrusion. However, to drive away visitors all the time (fig. 12), even if they only pay a visit through curiosity, or to steal twigs, might have a negative influence on the hatching of eggs. The likelihood of damage grows with the increase in the number of penguins living in the enclosure.

CONCLUSIONS AND DISCUSSION

Pair bond

The pair bond between the Black-footed Penguins of Artiszoo is very strong, 34 out of 35 examined birds paired with the same partner in successive years. There was only one penguin that changed her mate whilst her first partner was still present, but she eventually re-established the relationship after one season of unfaithfulness.

When a bird lost its mate for whatever reason, it usually found a new partner the following season.

Site tenacity

Like the penguin species *Eudyptula minor* and *Megadyptes antipodes* (Reilly & Cullen, 1981; Richdale, 1957) the Black-footed Penguins in Artiszoo have a tendency to breed each season in the same burrow (this is in agreement with the statement of Kearton, 1931, on this subject), but there was some shifting among available burrows. There is, however, no evidence to confirm the theory that penguins are more likely to shift after breeding unsuccessfully (Richdale, 1957) or the

theory that young inexperienced birds are more liable to shift than older experienced ones (Richdale, 1957). Here it should be noted that only a small amount of information exists on this subject concerning the penguins in Artiszoo, insufficient to draw any positive conclusions. Also, the ages of the partners of relatively inexperienced birds that have been examined are unfortunately unrecorded. However, it is very important to note this negative fact because it might be possible that an older experienced mate can perhaps compensate for any deficiency in the breeding behaviour of the inexperienced one (Richdale, 1957) and may even choose which burrow will be put to use.

There are indications that a burrow gets new owners only when the previous couple vacates it. This confirms the idea that it is an established habit among penguins that particular sites, burrows in this study, are "owned" by their inhabitants (Rand, 1963b). This habit eliminates competition among the more mature individuals. However, this feature in Artiszoo has the consequence that new nesters may not be able to establish themselves at all if the number of burrows is not adjusted every season according to the number of adults.

There is of course a limit to the number of birds that can breed in the enclosure of Artiszoo, one reason being that the Black-footed Penguin defends the immediate environs of its nest. Westphal & Rowan (1970) stated that there was no evidence to assume that maximum density of breeding pairs on the islands of South Africa ever exceeded the number of one breeding pair per sq. yd (1 yd^2 = 0.836 m^2). According to Rand (1963a) the penguins on Dassen Island breed at maximum densities of one pair every three sq. yds ($\pm$ 2.5 m^2). By comparison, a record of one pair per 4.8 sq. yds ($\pm$ 4 m^2) was attained in Artiszoo (on the largest of the two islands) in 1981. This is not to be considered as a natural phenomenon because both the number of adults present and the number of available nesting places are controlled by the zoo keepers.

Clutch size and number of clutches per season

The clutch size is normally two, one is much less common and three very rare. In three out of five cases in which a clutch consisted of three eggs, there were two females and one male that owned it.

Black-footed Penguins in Artiszoo lay two clutches per season in most cases, but one clutch per season is also very common. On all occasions that penguins laid three clutches, at least one of the clutches was unsuccessful and in about half of the cases one of the clutches consisted of only one egg.

Although table V indicates that the frequency of laying a second clutch was only slightly higher when first clutches were unsuccessful than when they were successful, I assume that this frequency was considerably higher in situations where the first clutch failed visibly, i.e. the eggs disappeared or were found to be broken at an early stage. The amount of available information on this subject is unfortunately too small to prove this assumption. The motive for my statement is the fact that the increase of the number of nesting places in which eggs were laid was out of proportion with the growth in the number of available adults (table VIII). This fact, together with the point that breeding couples shifted only in 10% of cases to another burrow within the season, and the indication that burrows receive new occupiers only when the previous owners have vacated them seems to leave no other conclusion than that the number of occupied burrows is a good approximation of the number of breeding pairs that actually had eggs, and that this is only a part of the total group of adults, especially in the seasons 1973 to 1979.

There was a distinct growth in the quantity of eggs produced in line with the increase in the number of adults during this period. However, the number of actual breeding birds remained very much the same from year to year. Therefore I drew the conclusion that the breeding couples were induced to produce second and sometimes even third clutches because more eggs disappeared or were found to be broken in an early stage when the number of adults grew. Probable causes will be discussed later.

When the eggs failed to hatch for reasons other than that they disappeared or were found to be broken, the eggs lay in the nests for more than

the complete incubation period, which lasts about 38 days (Lensink & Dekker, 1978). There are no indications to assume that the breeding birds dispose of their clutch as soon as they realize that the eggs will not hatch anymore, and the keepers collect the eggs only when they are obviously overdue and sometimes earlier when the eggs and the nests are deserted. It has never been recorded that penguins laid a second clutch while the first clutch that failed to hatch was still present. It is then, only after this interlude, that the breeding couple can start producing a second clutch in their burrow.

Breeding cycle

The breeding season in Artiszoo runs from August to May, and has two peak periods of egg-laying: one in August/September and one, less extreme, in December. A double peak in egg-laying was also reported for South Africa. Rand (1960 and 1963a) supposed that the species breeds twice a year and the months in which most eggs are produced are September and February/March. The situation at Dassen Island was described by Cooper (1980). There most eggs were laid in June and November/December in 1971—1972. Other colonies showed only a single laying peak, probably due to human disturbance. The gap between egg-laying peaks is much narrower in Artiszoo than in South Africa. A probable explanation for this difference is the shorter period during which the adults are allowed to guard the nestlings. In their natural habitat the nestling period lasts for about 80 days (Rand, 1960) with extremes of 64 and 105 days (Cooper, 1980), but in Artiszoo the young are taken from their nests at an age of around 42 days, thereby allowing the parents to reproduce that much earlier.

Data on re-nesting indicate that some pairs regularly lay in the first period (July-November) as well as in the second (December-March). The mean interval between successive layings was 4.5 months (range: 3 months 9 days—6 months 14 days, n = 28), for birds having raised one or two young to the age of 42 days in Artiszoo. This period of time is exactly the same for the mean interval between unsuccessful breeding attempts on Dassen Island (Cooper, 1980). This might be an indication that the penguins in Artiszoo are stimulated to lay a second and even third clutch by the enforced removal of the six-week old chicks from their nests.

Cooper (1980) reported a mean interval of 10.5 months (with a range from 8-13 months) between layings for successful pairs. This would imply a somewhat shorter cycle than one year. If the interval between breeding seasons for individual birds averaged always shorter than one year, a gradual shift of the laying peaks might be expected. In Artiszoo these peaks have only shown some oscillations, but are remarkably stable over the years, indicating that the birds generally have a strictly annual cycle. Data from other zoological gardens show sometimes a similar annual periodicity (e.g. Baltimore; Gailey-Phipps, 1978) and sometimes an almost continuous production of eggs without clear peaks (e.g. Antwerp; Van Bocxstaele, 1978).

The date of breeding varied from year to year, some years the first egg-production peak appeared in July/August and in others it appeared only in October. At this moment the causes of these shifts are unknown, but it could be caused by fluctuating temperatures and rainfall experienced during the course of a year. Anyway, according to Reilly & Cullen (1981) the differences in water temperature in Bass Strait are correlated with annual differences in the breeding success of the Little Penguin *Eudyptula minor* on Phillip Island, Victoria, and they stated that Boersma announced in 1976 and 1978, that for the Galápagos species of *Spheniscus, S. mendiculus,* the upwelling of cold water in the neighbourhood of colonies was associated with an outburst of breeding activity. Both observations make it interesting to investigate the relationship between the timing of the breeding season of penguins and the prevailing weather conditions.

Age of first breeding

At an age of between a half and two years the penguins in Artiszoo, both male and female, seem to develop an interest for companionship, which they fulfil by following and allopreening other birds repeatedly. When they reach the age of two years or more, they select a partner and

are ready to begin breeding. This is in complete agreement with the timing of first breeding of the Black-footed Penguins in South Africa, according to Jackson et al. (1976). In Artiszoo the actual timing of first breeding of individual birds is, apart from possible individual differences, strongly influenced by the number of available nesting places and by the structure of the population present at that particular time, e.g. a lack of adult males seemed to have postponed the first breeding of some adult females in the period 1976—1979.

Hatching success

One of the purposes of this study was to find the factors that influence the hatching percentage of eggs in Artiszoo, which was only 49.6% in the period 1966—1981 while the percentage of eggs that hatch in South Africa is 73.5% in burrows and 67.1% in open nests (Frost, Siegfried & Cooper, 1976).

Fig. 11 shows that the hatching success decreased with the number of adults present. In particular, there appeared to be a considerable drop in hatching success between 1971 and 1972 when the number of adults rose to well over 25. In comparing the periods 1966—1971 and 1972—1981 a significantly lower hatching rate was found in the latter period.

After examining several possible causes that could have influenced the hatching success I come to the conclusion that the decline of the breeding success after June 1972 was caused by the increase of the number of penguins living in the enclosure. The penguins tend to pay visits to breeding holes, sometimes through curiosity, and at other times to steal twigs and also to search for a proper nesting place (Kearton, 1931) or merely because they were frightened by something foreign in the enclosure (observations of F. A. Lensink and me during 1979/1980). The likelihood of damaging the eggs or disturbing the breeding process as a consequence of these visits grows with the increase of the number of penguins living in the enclosure. This negative influence on the hatching success of eggs is strongly enforced by a lack of burrows because the birds that want to breed but cannot find a proper nesting place keep searching for such a place. The increase in breeding success in 1980 and 1981 may in this view be explained by the fact that eight more burrows became available in 1980 and because adult penguins were sold that had had poor breeding results in the last years (2 couples in May 1980 and 3 couples and 1 breeding bird in May 1981).

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