Seasonal effects on nutrition, reproduction and aspects of thermoregulation in the Namaqua sandgrouse (*Pterocles namaqua*)

by

John Dixon

Nature Conservation and Tourism Division, P.O. Okaukuejo, 9224, South West Africa

and

Gideon Louw

Zoology Department, University of Cape Town, Rondebosch, 7700

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ABSTRACT

On the basis of both field observations of nesting birds and detailed chemical and morphological studies on 10 birds (5♂ and 5♀) per month, it would appear as if *P. namaqua* favours the cooler winter months for breeding in the Namib Desert Park. In view of the simple nature of the nest scrape and studies on the thermoregulatory behaviour of this species, we have concluded that soil-surface temperatures play a critical role in determining the success of breeding. Preferred food items are the highly nutritious, but minute seeds of *Tephrosia dregeana* and two species of *Cleome*. Neither the abundance of these plants nor rainfall appear to be important cues in the synchronisation of the main breeding season. Observations on hormone plasma levels, gonads, fat index, thyroid activity, vitellogenesis, water consumption by chicks and a theoretical energy budget have also been described.

1 INTRODUCTION

Although sandgrouse have been a popular subject for investigation by ornithologists for many years (Christensen, 1964) and the subject of detailed study in recent years by Cade and Maclean (1967) and Maclean (1968), no attempt has as yet been made to examine the relationship between nutrition, reproduction and thermoregulation in detail. The main purpose of this study was, therefore, to investigate the effects of season and climate within the desert environment upon the reproductive biology of the Namaqua sandgrouse. While engaged in this study it was, however, also possible to collect additional data in regard to nutrition, thermoregulation and the behaviour of this interesting species. Two separate studies on the taxonomy of the sandgrouse and the suitability of this species as a game bird have also been carried out and will be reported elsewhere.

2 PROCEDURE

The Namib Desert Park was chosen as the general study area. Monthly samples were taken for a period of 12 months. Each sample consisted of five females and five males and was collected within a triangle bounded by three water-holes, namely, Hotsas, Ganab and Zebra Pan (See Map 1). This area has a mean annual rainfall of less than 100 mm and is characterised by intense solar radiation, high soil temperatures but relatively cool moist ocean winds which are frequently experienced in late afternoon (Seely and Stuart, 1976). Vegetation is sparse, and fluctuates dramatically in response to sporadic thunder-showers which occur most frequently during late summer. This vegetation is dominated by drought-resistant perennial and annual grasses.

MAP 1: Map of the study area. Most birds were collected within a triangle bounded by Hotsas, Ganab and Zebra Pan.

Adult birds were shot at random while flying into water-holes in the early morning with due allowance being given to the number of each sex required. Most of the samples were collected at Hotsas but on occasion, when birds of specific physiological status or age group were required, they were hunted along the washes east of Mirabib.

The following data were recorded:

2.1 Body weights

2.2 Body measurements
- Wing length
- Tail length
- Tarsus
- Culmen

2.3 Reproductive data
- Testis mass and histology
- Ovarian mass, macroscopic and microscopic morphology
- Plasma proteins with special reference to vitellogenesis using cellulose acetate electrophoresis
- Plasma hormone levels of testosterone and oestradiol — 17B using radio-immunoassays
- Thyroid cell height and follicular size
- Sexual behaviour
- Nesting frequency

2.4 Nutrition
- Mass of crop contents
- Analysis of crop contents

Identification of food plants
Chemical analysis of food plants using an adiabatic bomb calorimeter and the A.O.A.C. method for proximal analysis.
Water consumption and ratio of sexes drinking
2.5 Thermoregulation
Body temperatures using fast registering Wesco thermometer
Nest temperatures using YSI telethermometer and field recorder
Thermoregulatory behaviour
2.6 Predators
2.7 Moulting
2.8 Fat index
2.9 Environmental data
Temperature
Rainfall
Quality of vegetation

3 RESULTS AND DISCUSSION

3.1 Body weights and measurements

Body weights were usually measured after removal of a 1 ml blood sample as well as the thyroids and gonads. These weights can therefore not be considered accurate and were merely used for comparative purposes when comparing monthly samples. No definite seasonal trends were observed from these observations. Nineteen adult birds were, however, weighed immediately after being shot and they ranged in weight from 153,6 – 214,3 g with a mean weight of 186,2 g.

Measurements of wing, tail, culmen and tarsus length were made on freshly killed birds and not on study skins. Tail measurements did not include the length of the pin feathers as these are subject to considerable and variable amounts of wear from contact with the ground surface. The mean culmen length for male and female birds was 13,2 mm and 13,3 mm respectively, while the mean tarsus length was 21,6 mm for the males and 20,4 mm for the females. Mean wing and tail length for the male birds was 170,0 mm and 82,3 mm respectively which was somewhat greater than the values obtained for female birds, namely 165,1 mm and 79,3 mm respectively. Again, as expected, no seasonal association with body measurements was observed and these data compare reasonably well with those reported previously (Clancey, 1967).

3.2 Reproductive data

All nesting records available for this species were obtained from the Percy FitzPatrick Institute for African Ornithology and analysed on a monthly basis. These data show clearly that, apart from the months of March and May nesting records exist in southern Africa for *Pterocles namaqua* for all the remaining months. Moreover, it would also appear as if breeding activity begins to increase rapidly during June and July to reach a peak between August and November (Spring) with a steady decline from December to May. As these records are from summer-rainfall areas it would seem as if rainfall is not the primary environmental cue for sexual activity in this species and that it is possible for *P. namaqua* to breed throughout the year even though at a greatly reduced intensity. Maclean (1968) reports that *P. namaqua* showed breeding peaks during July and November in the Kalahari Gemsbok National Park. These were dry months and examination of his data reveals that most of the breeding in this species occurs during the cooler months of the year.

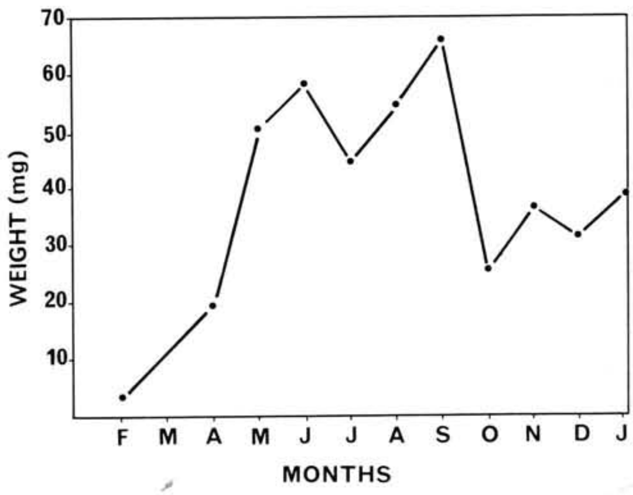

FIGURE 1: Seasonal variation in mean testis weight.

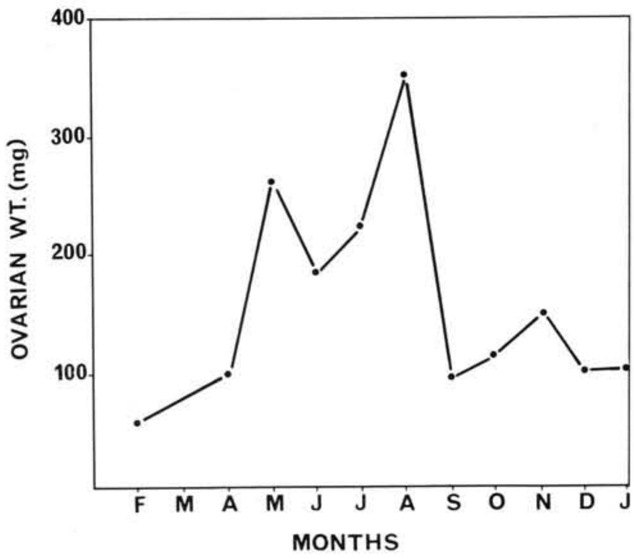

FIGURE 2: Seasonal variation in mean ovarian weight.

Our study on the breeding biology of this species in the Namib Desert Park (Figs. 1 and 2) shows a reasonably similar pattern to that of Maclean (1968) with a high intensity of sexual activity during spring. However, this increased activity began as early as May and was sustained during the winter months of June and July to extend through to the Spring in September. Moreover, the initial rise in activity during April was preceded by thunder showers which caused a flush of green growth in the study area. Also, while sexual activity was at a minimum during January and February of 1973 (which were dry months), breeding activity during these same months in 1974 was moderately high. The latter activity in 1974 was accompanied by thunder showers and moderately cool weather with low soil temperatures which were absent during 1973. It would appear then that, although *P. namaqua* will breed almost throughout the year, the winter months are by far the most favoured months of the year. Moreover, breeding takes place independently of rainfall but rainfall and the accompanying cooler conditions during the hot summer months may favour a moderate intensity of out-of-season breeding.

In the above discussion the criteria used for sexual activity were primarily weight and histological appearance of the gonads as well as the occurrence of nesting birds. These data are presented in graphic form in Figs. 1, 2 and 8. Weight of ovaries followed a reasonably similar pattern to that of the testes but variable amounts of yolking caused too great a standard deviation to rely on this criterion alone. The occurrence of nesting pairs, chicks and fledglings also followed the pattern of testis weight closely.

Plasma protein analysis of female plasma showed increased vitellogenesis during the surge in increased sexual activity during April and May, 1973, shortly after rain had fallen. This criterion would appear to be a sensitive and early index of an impending increase in sexual activity, as it is a result of increased oestrogen secretion in the female. This in turn results in mobilisation of proteins by the liver for the yolking follicle.

However, after the initial surge in vitellogenesis, results became very variable throughout the remainder of the study period. The latter result may have been influenced by varying ages and therefore degree of sexual maturity in the sampled population.

During the course of the investigation extremely sensitive radio-immunological methods were developed to assay plasma levels of male and female hormones, namely testosterone and oestradiol-17B. These methods allow the detection of as little as 10^{-9} g of hormone per ml of blood. In spite of this sensitivity many of the samples gave negative values and apart from a slight increase during the initial surge in sexual activity, the results obtained were very variable. Very little work of this nature has been attempted before but preliminary results on domestic birds seem to show that female hormones are released only fleetingly into the plasma and that generally the plasma levels of these hormones is surprisingly low in birds. In a similar study on cormorants by Berry (1976), he obtained a close correlation between testis size and plasma levels of testosterone during the breeding season. He, however, was able to obtain uniformly large blood samples from an exclusively adult population. His results on plasma levels of oestradiol-17B were as variable as in the present investigation.

Examination of thyroid weights and acinar cell heights showed a tendency for thyroid weights to decrease with a concomitant increase in acinar cell height during the winter months when sexual activity was most intense. These data also fit the pattern of a decrease in the fat index during the same period but the variation within months was too great to obtain definite statistical proof of this phenomenon.

3.3 Nutrition and Water

Analysis of the crop contents of adults, juveniles and recently hatched chicks have provided interesting data on the feeding habits of *Pterocles namaqua* in the Namib Desert Park.

From these studies it became clear that the diet of this species in the Namib Desert Park is restricted to the very small seeds of seven plant species with the very occasional appearance of green vegetative material (*Zygophyllum cylindrifolium* and *Sesuvium sesuvoides*) and flower buds in the crop contents. At first the appearance of green material (young leaves of *Z. cylindrifolium*) was thought to be associated with the sudden increase in sexual activity recorded in May after the rains during April. Subsequently, however, peak sexual activity was recorded much later while green vegetative material was entirely absent from the crop contents.

The minute seeds which dominate the diet of *P. namaqua* are in some cases as small as the sand grains covering the desert plain. If we accept that the olfactory sense in birds is very ineffective then it is noteworthy that these animals are capable of gleaning this remarkably cryptic material from the sand grains (Plate 1). Of the seven specific types of seeds taken by *P. namaqua* the most important species are *Tephrosia dregeana*, *Cleome diandra* and *Cleome luederitziana*. The remaining four could not be identified on the basis of seed morphology.

TABLE 1: Gross energy and protein content of seeds consumed by *P. namaqua*. (Dry weight basis)

Species	Gross Energy (cal g)	Crude Protein (%)
Tephrosia dregeana	5022	32
Cleome diandra	5059	16
Cleome luederitziana	5129	16

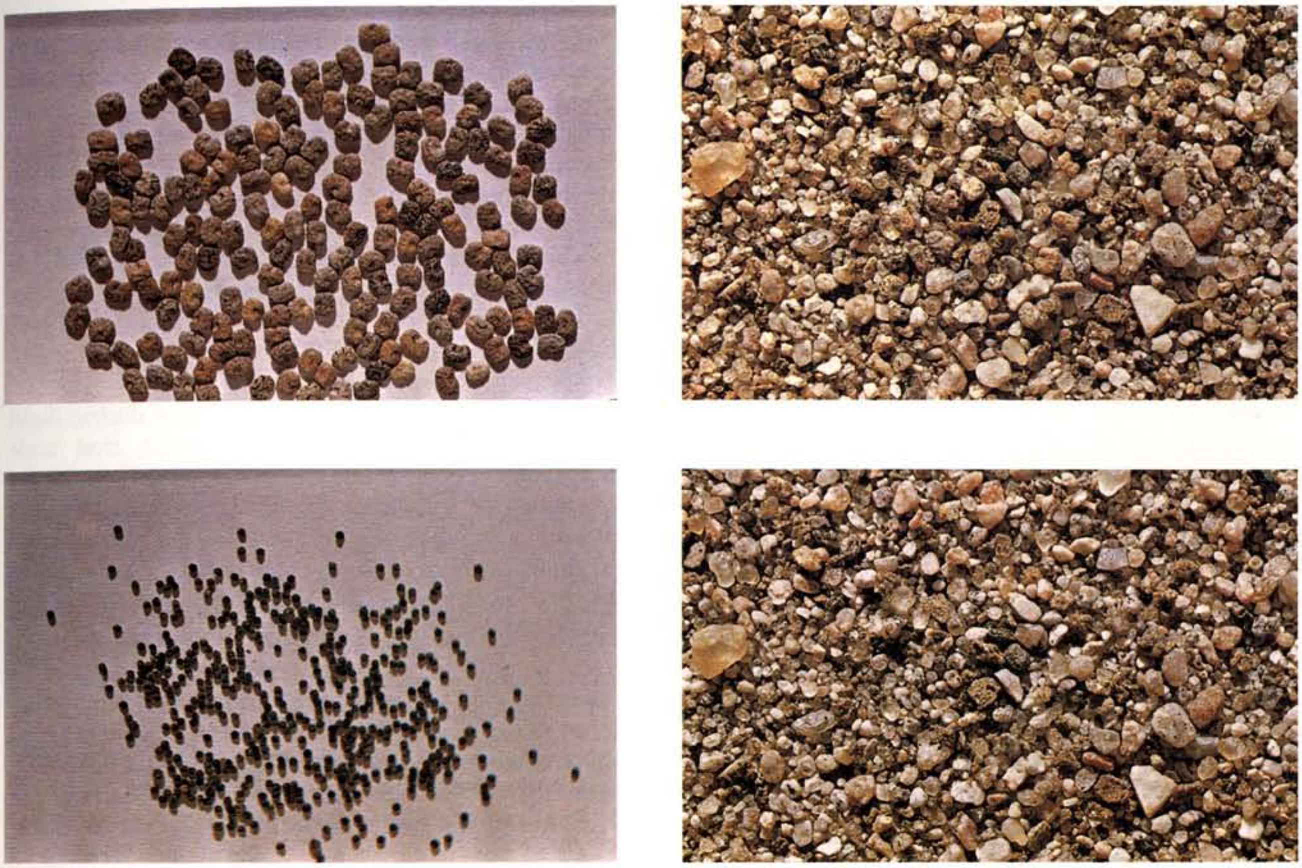

PLATE 1: Illustrating the extremely cryptic nature of the seeds which form the major constituent of the diet of *P. namaqua*: a) *Tephrosia dregeana* alone, b) *Tephrosia* mixed with natural substrate, c) *Cleome luederitziana* alone, d) *Cleome* mixed with natural substrate.

The gross energy values and protein content of the three main species was determined and the results are given in Table 1. These values are extremely high for plant material and compare favourably with the gross energy values obtained in energy-rich seeds such as soya beans (5 520 cal / g) and are considerably higher than the standard value for starch (4 230 cal / g). The latter fact suggests that the seeds have a high oil content. The protein content, particularly that of *Tephrosia*, is remarkably high and it can be concluded that the diet of *P. namaqua* is most nutritious.

The variation in weight of the crop contents by months is graphically illustrated in Fig 3. Although the highest values were recorded in May and September which were also months of peak sexual activity, the variation during the winter months when sexual activity remained high, precludes any definite association between weight of seed-intake and breeding activity. Moreover, an analysis of the various types of seeds, appearing in the crop, showed no definite association with sexual activity. In fact the diet of *P. namaqua* remains surprisingly constant throughout the year with no dramatic change in either the food of the adults or the chicks, which could be associated with an environ-

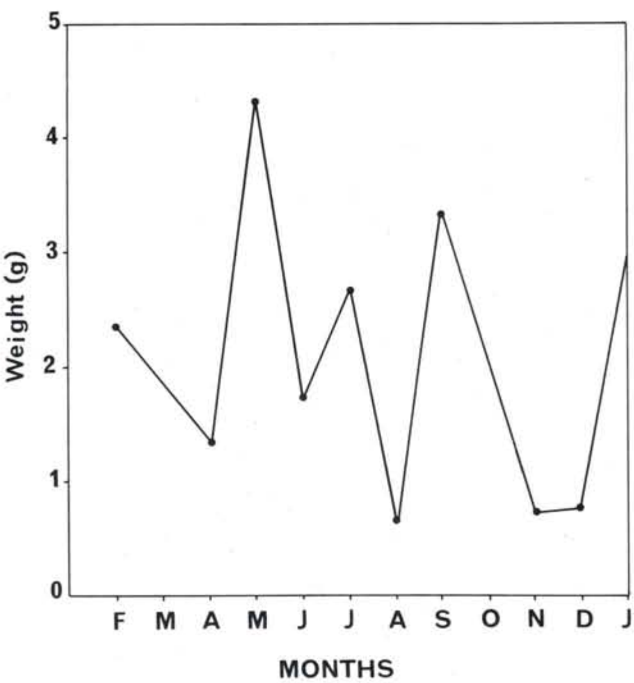

FIGURE 3: Seasonal variation in weight of crop contents.

mental cue for sexual activity. It should, however, be noted that the abundance of food plants is definitely much increased after rain. Nevertheless, once the plants have seeded the seeds remain on the surface of the desert plain and, although they could be used by small mammals and other birds, are theoretically available throughout the year. This fact further strengthens the argument that food availability is unlikely to be an important environmental cue for synchronisation of breeding activity. Also it is significant to note that grass seeds never appeared in the crops of the birds in spite of the relatively luxuriant growth of grass which occurred after thunder showers during the study period.

Energy requirements of wild birds are not well documented but if we accept Lasiewski and Dawson's (1967) equation where log M = log 78,3 + 0,723 log W (M = metabolism in k cal / day; w = body weight in kg), then it is probable that the standard metabolic rate of *P. namaqua* will approximate 23,2 k cal / day. If we now allow a total flying time of 4 hrs per day and a twelve-fold increase in metabolic rate during flying and a three-fold increase during foraging for 8 hours, then the probable daily energy requirement of a 182 g *P. namaqua* should approximate 80,7 k cal / day. If we now consider the energy-rich nature of the diet of *P. namaqua* discussed previously, then it is clear that the above estimated energy requirements could be met by only 15,7 g of *Cleome luederitziana* seed if they were fully digested. Allowing for a digestion coefficient of 80 % then the daily requirement would increase to 19,6 g. The relative abundance of these food plants which produce energy-rich seeds is very apparent, even to the casual observer who walks along any of the washes in the study area. It is therefore not surprising that at certain times of the year the Namib Park is able to support such spectacularly large flocks of *P. namaqua.*

Finally it should be noted that insects and crop milk were never present in the crops of this species and that the diet of the newly-hatched chicks was in most cases identifical to that of the adults. Maclean (1968) is also of the opinion that both *P. namaqua* and *P. burchelli* feed exclusively on small hard seeds throughout their lives in the Kalahari Gemsbok National Park.

3.4 Water consumption

We were not able to measure the water intake of adult birds and did not study the intriguing feather-wetting behaviour in any detail as the latter has been studied elsewhere (Cade and Maclean, 1967). We were, however, able to show that the ratio of males to females was much higher at the water-holes in the mornings during the breeding season (6,6 : 1,0 as opposed to 1,16 : 1,00 during the non-breeding season). These data are in general agreement with those of Maclean (1968) collected in the Kalahari. Also while collecting chicks to examine their crop contents we were able to measure the volume of the water in the crop. This amount varied from zero to 3 ml and in some cases amounted to as much as 30 % of the chick's body weight at 16h00. If we accept that the male parent carries out wetting of the breast feathers mostly during the morning (as revealed by previously discussed sex ratio counts) then the occurrence of 3 ml in the crop of chicks in the late afternoon is indeed a remarkable adaptation to scarcity of and infrequent access to water in the desert environment. Cade and Maclean (1967) have shown that the belly plumage of a dead sandgrouse can absorb as much as 20 to 40 ml of water. They then allowed for evaporative losses during flight and calculated, using a physical model, that male sandgrouse could deliver as much as 10 to 18 ml of water to the chicks. If we then accept that the maximum number of chicks hatched by *P. namaqua* is three, then our observations of an intake of at least 3 ml are therefore well within the theoretical calculations of Cade and Maclean (1967).

3.5 Thermoregulation

Cloacal temperatures collected from freshly killed adult birds were within the narrow but expected range of 41,5 – 42,0°C. Newly hatched chicks, however, were found to be thermolabile in spite of their precocity. For example at 16h00 at an ambient temperature of 20,5°C two chicks had cloacal temperatures of 32,4°C and 33,8°C respectively. While at 12h45 at an ambient of 28,0°C the cloacal temperatures of three chicks ranged from 37,2°C to 39,1°C. In contrast with the above, juvenile birds which had just begun to fly had temperatures within the adult range of 41,0 – 42,0°C.

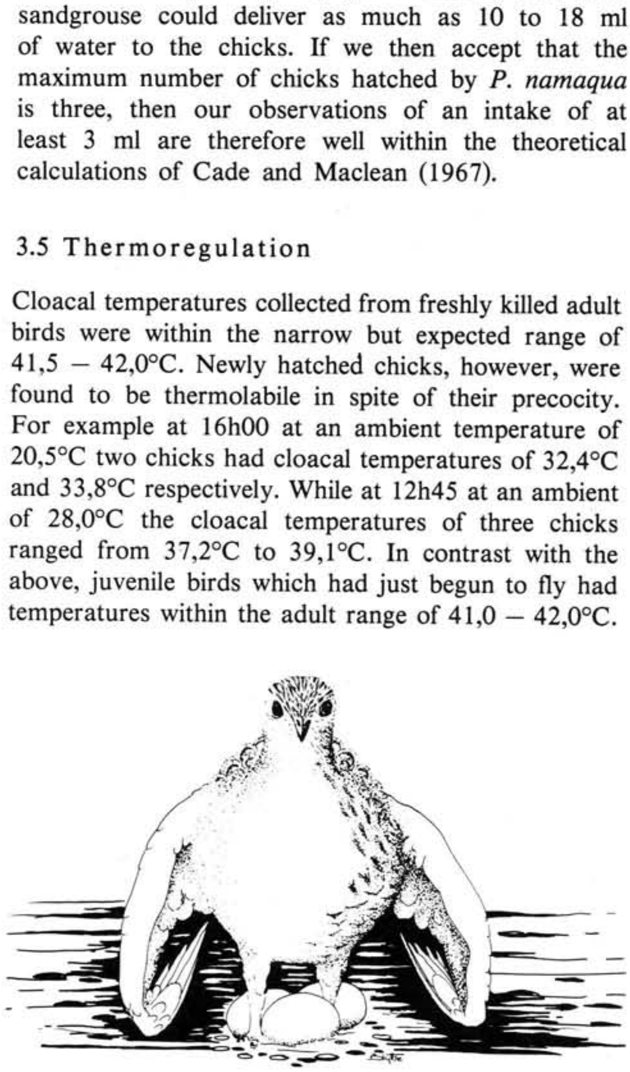

FIGURE 4: Under high ambient temperature conditions *P. namaqua* frequently faces into the cool south west wind, raises itself from the nest, and adopts the above posture to facilitate convective cooling of the eggs.

Thermoregulatory behaviour in *Pterocles namaqua* is best exemplified by incubating birds on the nest. When ambient temperatures exceed the thermal neutral zone the birds employ a variety of strategies to lose heat or minimise heat gain. For example, they will orientate

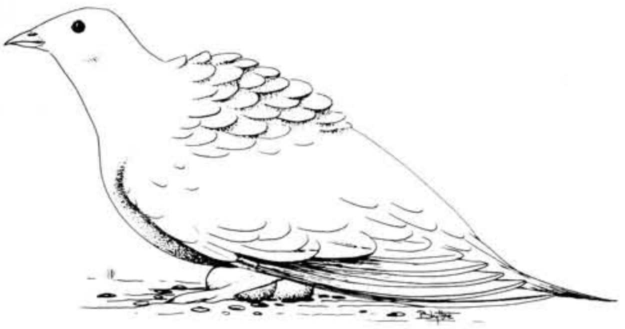

FIGURE 5: While incubating under high ambient temperature conditions, *P. namaqua* frequently raises the mantle feathers to increase the insulation of the body against intense solar radiation.

their bodies so that the head is facing towards the sun, thus minimising the surface area exposed to direct radiation. However, if wind, particularly cool south west winds from the ocean, are blowing, they usually face into the wind with raised wings in order to facilitate convective cooling (Fig 4). Under these circumstances the whole body is occasionally raised from the nest, presumably to allow convective cooling of the eggs while the eggs remain in the shade of the body. While in this position the birds may raise the wings with the humeri in a horizontal plane, but with the primaries resting on the soil surface. Simultaneously the mantle feathers on the back are raised providing an air space between these feathers and the bird, Fig 5. The above behavioural responses to high ambient temperature will increase insulation against direct solar radiation and optimise convective cooling. Finally, evaporative cooling is employed by very rapid gular fluttering. The main advantage of gular fluttering over thermal panting is that the former requires far less energy expenditure, whereas thermal panting, involving the muscles of the rib cage, results in increased metabolism and therefore adds to the already critical heat load. One therefore gains the impression that the incubating birds, particularly towards the end of winter when soil temperatures start rising, are driven to the critical limits of their thermoregulatory capacity to keep their eggs cool.

These thermoregulatory mechanisms are sufficient to maintain the nest temperature below the presumed critical temperature which would result in embryonic death, provided that the soil surface temperatures are not excessively high. The nest of *P. namaqua* is merely a very shallow scrape on the surface of the soil and, as no insulation is present in the form of woven grass or other material, the eggs are virtually resting on the surface of the soil and surface soil temperatures must therefore be considered a critical factor in the breeding success of this species.

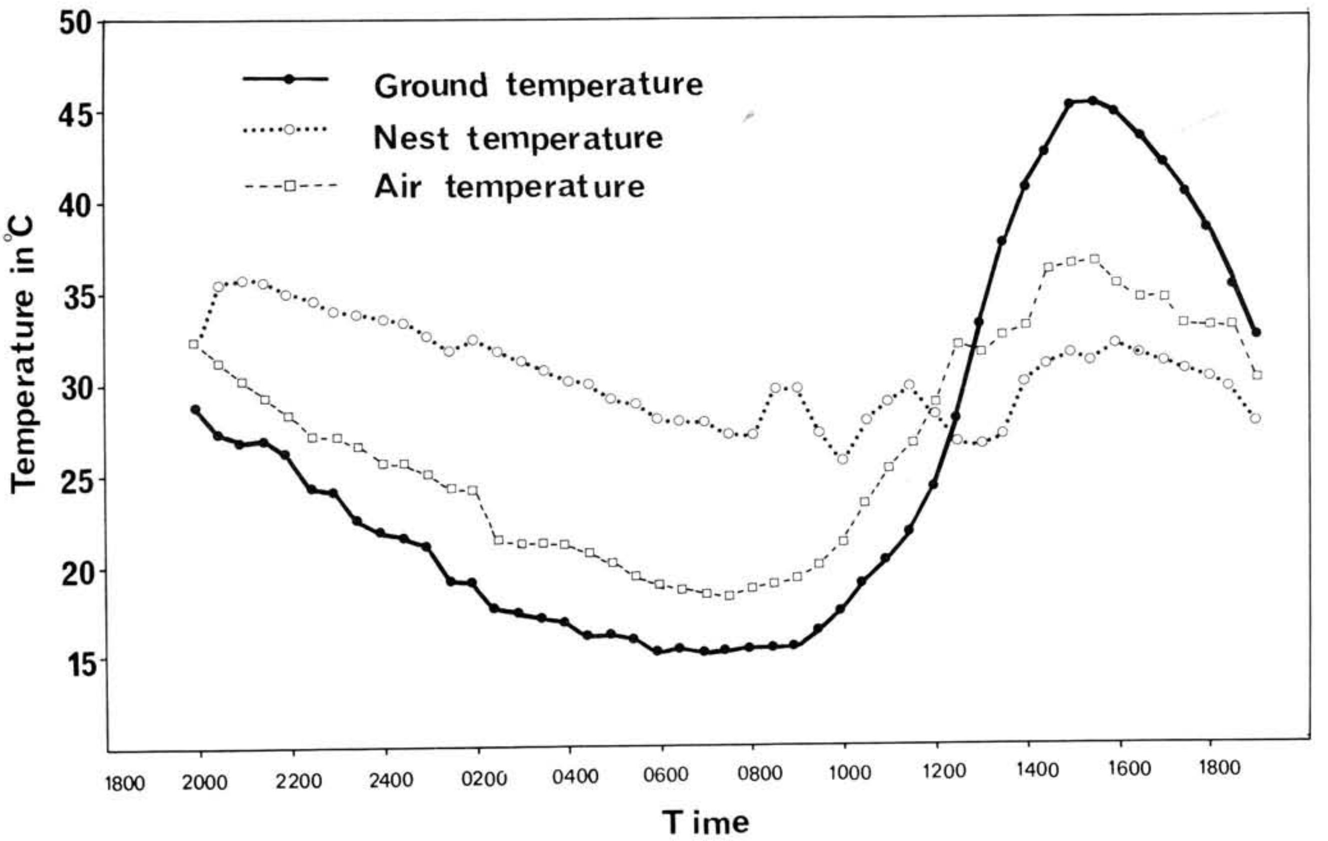

FIGURE 6: When soil surface temperatures do not exceed 50°C, *P. namaqua* is able by behavioural and physiological thermoregulation to maintain egg surface (nest) temperature below 40°C.

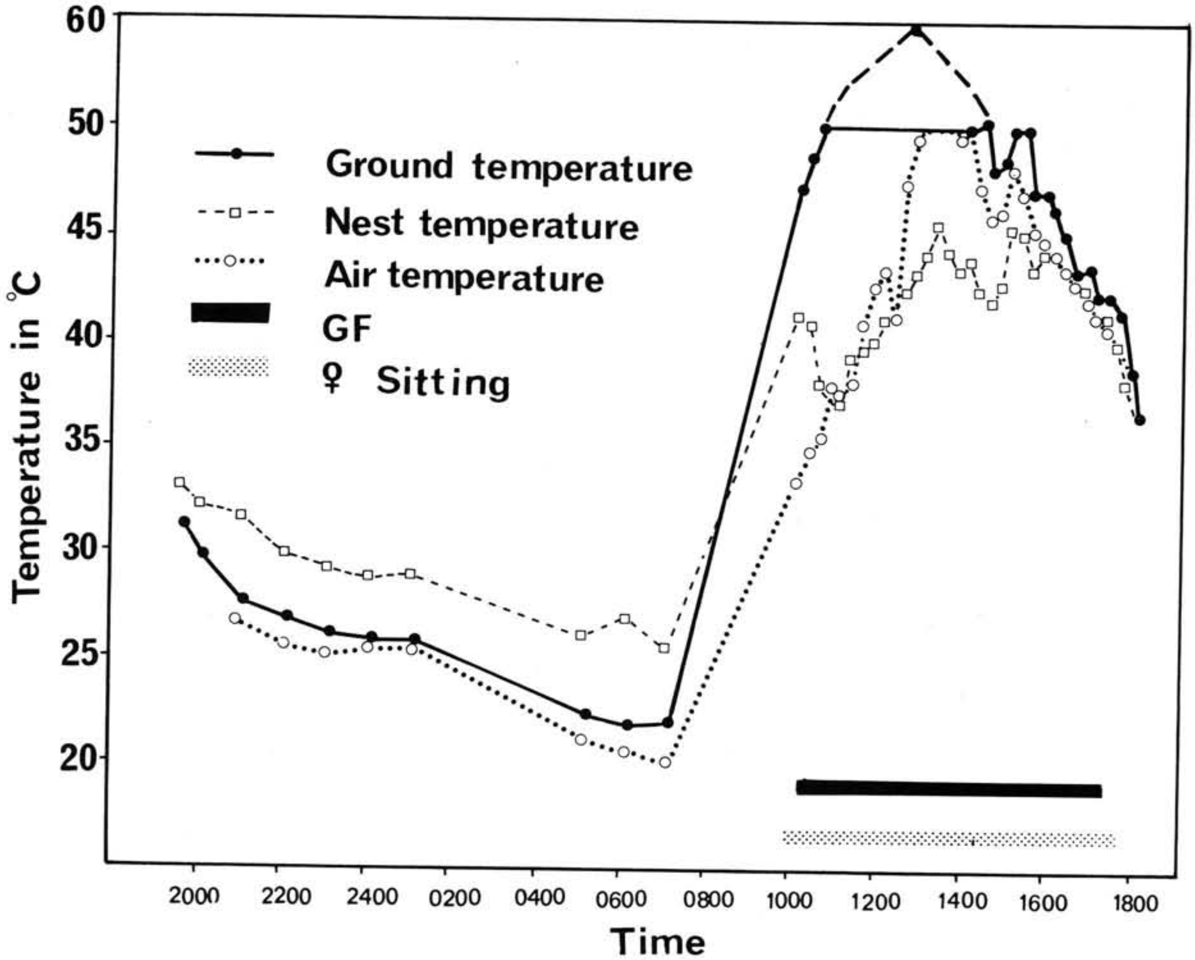

FIGURE 7: When soil surface temperatures exceed 50°C, *P. namaqua* is no longer able to maintain egg surface (nest) temperatures below 40°C.

To investigate this question, nest (surface of eggs), soil surface and air temperatures were taken continuously by means of a YSl telethermometer and suitable thermistor probes over a period of 24 hours in several nests. These results have been summarised graphically in Figs. 6 and 7.

The data contained in Fig 6 were collected when prevailing soil temperatures were within reasonable limits (15 – 46°C). Under these conditions the birds had little difficulty in maintaining nest temperatures within very favourable limits, the maximum never exceeded 37°C. In contrast, the data in Fig 7, obtained from another nest at a later date, shows that when soil temperatures approach 60°C the birds are unable to cope with the situation and nest temperatures exceed 45°C in spite of intense thermoregulatory behaviour on the part of the incubating bird. The developing embryos were examined from this nest and it was evident that they had not survived. Moreover, it should also be borne in mind that excessively high surface temperatures do not only affect the developing embryos but must also play a critical rôle in the survival of the newly-hatched, thermolabile chicks.

Although a continuous record of surface soil temperatures was not available within the study area, these data were available from the nearby weather station at Gobabeb. These records show that during the cooler months of May to September the monthly means at 14h00 do not exceed 49,3°C and that the range was 41,7 – 49,3°C. In contrast the temperature range during the hotter months (February, March, April, October, November, December and January) was 54,3 – 58,9°C. It is therefore not surprising to learn from the reproductive data discussed previously that maximum sexual activity was recorded during the cooler months from May to September (See Figs. 1, 2 and 8).

Another bird, which also incubates eggs in an uninsulated scrape within the Namib Park is the ostrich (*Struthio camelus*). These birds breed successfully during the hotter months after rain in spite of high soil surface temperatures but it must be remembered that they weigh approximately 90 kg in contrast to the 180 g of *P. namaqua* and therefore have a far greater thermal inertia with which to overcome the unfavourable thermal gradient.

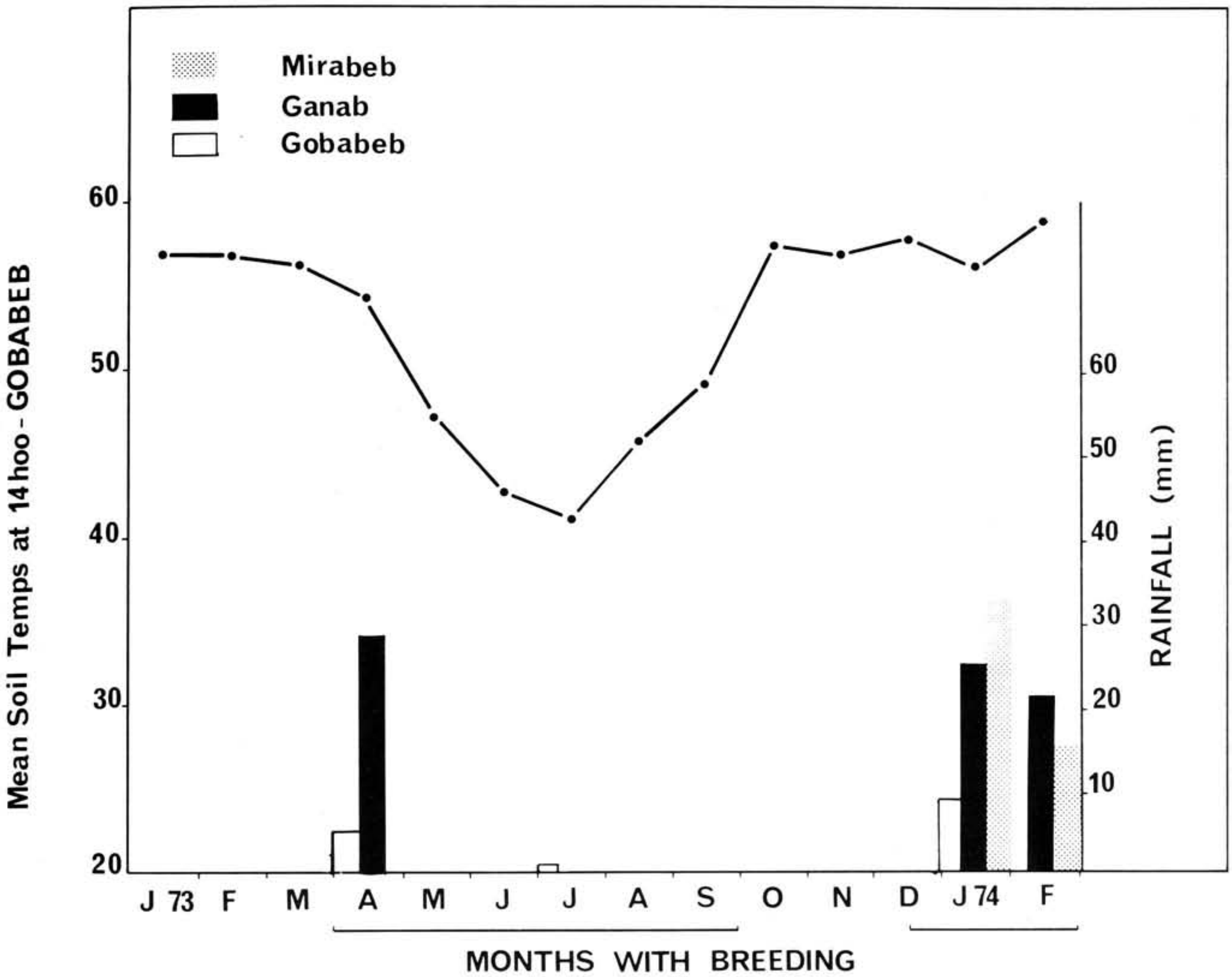

FIGURE 8: Relationship between mean soil surface temperatures at 14h00, rainfall and the occurrence of nesting *P. namaqua* in the Namib Desert Park.

3.6 Predation

During the study period the following predators of adult birds were recorded; Lanner falcon and black-breasted snake eagle. In addition black-jacked jackals were observed to prey upon both eggs and chicks, while the greater kestrel and pied crow were seen to prey on chicks. However, no seasonal change in predation intensity was recorded which could explain why *P. namaqua* should favour the winter months for breeding.

3.7 Moulting

Analysis of the moulting cycle in *P. namaqua* showed that there was no distinct moulting season. Furthermore, it was clear that sexually active birds showed signs of moult. It would appear therefore as if *P. namaqua* is capable of moulting while in a breeding condition. The data, however, did not allow us to confirm if birds engaged in active breeding were con-

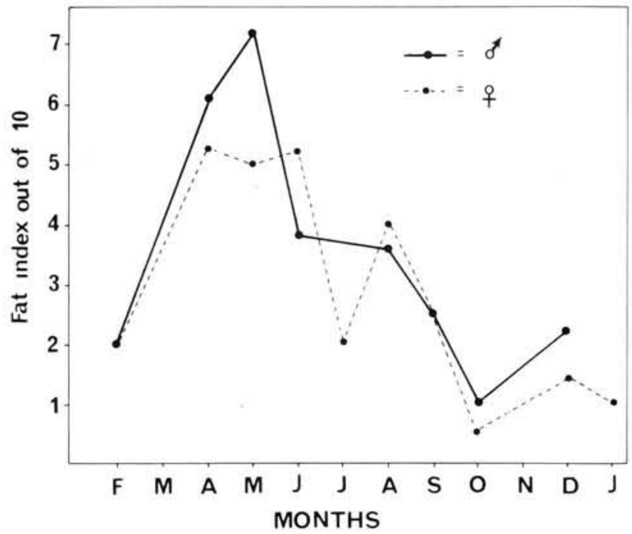

FIGURE 9: Seasonal variation in fat index (visually appraised by scoring dissected animals from 1 to 10).

currently undergoing moult (Table 2). These findings are in general agreement with the observations of Clancey (1967) who maintains that the main breeding season for *P. namaqua* coincides with the cooler months of the year and that most birds moulted from May to August.

TABLE 2: Seasonal pattern of moulting in *P. namaqua*. Primary feathers in right wing are numbered from the medial to the most lateral position in ascending order. Scoring of new growth in feathers was as follows: 0–10% = 1; 10–30% = 2; 30–60% = 3; 60–90% = 4; complete new feathers scored 5 and old feathers scored 0.

			1	2	3	4	5	6	7	8	9	10
January	101	♀	2	0	0	0	0	2	0	0	0	0
February	5a	♀	5	5	5	0	0	0	0	0	0	0
	102	♀	5	5	0	0	0	0	0	0	4	0
	104	♀	0	0	0	0	0	0	0	4	0	0
	105	♀	5	5	4	0	0	0	0	2	0	0
	108	♀					no moult					
	109	♀	5	5	5	5	5	5	5	2	0	0
	114	♀	5	5	5	0	0	0	0	0	0	3
	116	♀	5	5	5	5	5	5	5	3	0	0
	4	♂					no moult					
	103	♂	5	5	5	5	5	4	0	0	0	0
	106	♂	5	5	5	3	0	0	0	0	0	0
	111	♂	5	5	5	4	0	0	0	0	0	0
	112	♂	5	5	5	5	5	5	5	4	0	0
	113	♂	5	5	5	5	5	5	5	0	0	0
	115	♂	5	5	5	0	0	0	0	0	0	0
	117	♂	5	5	5	5	5	5	5	5	5	0
	118	♂	5	5	5	5	5	5	5	0	0	0
	119	♂	0	0	4	0	0	0	0	0	4	0
May	20	♂	0	0	0	0	1	0	0	0	0	0
	22	♂					no moult					
	25	♂	1	5	5	5	5	0	0	0	0	0
	28	♀	0	0	0	3	0	0	0	0	3	0
June	29	♀	5	5	5	5	5	5	5	5	4	0
	31	♀					no moult					
	34	♀					no moult					
	35	♀					no moult					
	37	♀					no moult					
	30	♂					no moult					
	33	♂					no moult					
	38	♂	5	5	5	5	0	0	0	0	0	0
	39	♂	5	5	5	5	5	5	5	5	5	0
	40	♂	5	5	5	5	5	5	5	0	0	0
July	43	♀					no moult					
August	56	♀					no moult					
	57	♀	5	4	5	5	5	5	5	5	4	0
	1352	♀	5	5	5	5	0	0	0	0	0	0
	1353	♀	5	5	5	5	5	5	4	0	0	0
	1354	♀	5	5	5	5	5	5	0	0	0	0
	1355	♀					no moult					
	1356	♀					no moult					
	1357	♀	5	5	5	5	5	5	4	0	0	0
	1358	♀					no moult					
	1344	♂	5	5	0	0	0	0	0	0	0	0
	1345	♂					no moult					
	1346	♂	5	5	5	5	5	1	0	0	0	0
	1347	♂	1	5	0	0	0	0	0	0	0	0
	1348	♂	5	5	5	5	4	0	0	0	0	0
	1349	♂	5	5	5	5	5	5	0	0	0	0
	1350	♂	0	0	0	1	0	0	0	0	0	0
	1351	♂	0	0	2	0	0	0	0	0	0	0
September	65	♀	5	5	5	3	0	0	0	0	0	0
	66	♂	5	5	5	0	0	0	0	0	0	0
October	69	♂	5	5	5	5	0	0	0	0	0	0
	72	♂	5	5	5	5	0	0	0	0	0	0
	70	♂	5	5	5	5	0	0	0	0	0	0
	71	♂	5	5	5	5	5	0	0	0	0	0
	73	♀					no moult					
December	78	♀	5	5	5	5	5	1	0	0	0	0
	79	♀					no moult					
	81	♀	5	4	0	0	0	0	0	0	0	0
	82	♀	5	5	5	1	0	0	0	0	0	0
	83	♀	5	5	5	5	5	2	0	0	0	0
	84	♀	5	5	5	5	5	0	0	0	0	0
	86	♀	5	5	5	5	5	0	0	0	0	0
	88	♀	5	5	0	0	0	0	0	0	0	0
	91	♀					no moult					
	92	♀	0	0	0	0	0	0	0	0	3	0
	93	♀	0	0	4	0	0	0	0	0	0	2
	98	♀	0	0	0	0	0	0	0	0	0	0
	74	♂	5	5	5	5	5	0	0	0	0	0
	75	♂					no moult					
	76	♂	5	5	5	5	5	0	0	0	0	0
	77	♂	5	5	5	5	5	5	0	0	0	0
	80	♂	0	0	0	4	0	0	0	0	0	0
	85	♂	5	0	0	0	0	0	0	0	0	0
	87	♂	5	5	5	5	0	0	0	0	0	0
	89	♂	5	5	5	5	5	0	0	0	4	0
	90	♂	0	0	0	0	0	0	0	1	0	0
	94	♂	5	5	5	5	5	5	5	0	0	0
	96	♂	5	5	5	5	5	5	5	5	0	0
	100	♂					no moult					

3.8 Fat index

The amount of fat in the sampled birds was visually appraised by assigning a score of 1 to 10 points. The results have been summarised graphically in Fig 9 and show that a marked increase in fat deposition occurred during March to reach a peak in April just prior to onset of the peak in sexual activity during May. Sexual activity, was, however, maintained at a high level throughout the winter and during this time a steady decline in fat content occurred.

It would appear therefore that in spite of the abundance of food plants during this period (See nutrition section) the increased energy requirements during the breeding season exceeded the energy intake and fat content declined in both sexes. The sudden increase in fat content during March is, however, not as easy to explain, as it occurred before the onset of significant rainfall. This observation again emphasises the independence of the birds upon availability of food as an environmental cue for synchronisation of the breeding season. It is therefore possible that the declining photoperiod during February may be involved by influencing the endocrine system, which in turn could bring about the necessary metabolic changes.

3.9 Environmental data

Data in respect of mean monthly rainfall and mean monthly soil surface temperatures at 14h00 are presented in Fig 8. These data again confirm that breeding activity in *P. namaqua* is not as closely associated with rainfall as would be expected but, as pointed out previously, occurs when soil surface temperatures are reasonably low.

4 ACKNOWLEDGEMENTS

We wish to thank the Director of the Division of Nature Conservation and Tourism in South West Africa for permission to carry out this study and for logistic support. The CSIR is thanked for financial assistance for the laboratory studies. The following are also thanked for their assistance provided in various ways: M. K. Seely, B. Sandelowsky, W. Veith, D. Mostert and Sandra Hardman.

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