

Daily patterns of behaviour compared between two sand-grouse species (*Aves: Pteroclididae*) in captivity

by

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1 INTRODUCTION

Sand-grouse of various species are characteristic occupants of the arid and semi-arid zones of Africa, the Middle East and central-southern Asia. They have diversified into several groups of sympatric species and may become extremely abundant in environments of generally low biological productivity and of thermal extremes. Therefore, they must be judged as successful inhabitants of these difficult habitats, and knowledge of their biology is important if one is to understand the spectrum of adaptations amongst animals living in such extreme environments.

Interest in sand-grouse biology has quickened in the last two decades, with substantial publications by Christensen, Bohl & Bump (1964), Maclean and his associates (see Maclean, 1968, 1976), George (1969, 1970), Thomas & Robin (1977), Dixon & Louw (1978), and several other articles. Naturally, much of the work reported centres on observations at water-holes and at nests, where the birds are most easily seen, and there is much less information on their behaviour elsewhere and under other circumstances. In our experience, reliable prolonged field observations of non-breeding birds are extremely difficult to obtain because of the bird's cryptic, elusiveness and wary disposition. Therefore, we kept a group of wild-caught adult birds in a large aviary where they could be studied with minimum disturbance at any chosen time. The results of these observations are

ABSTRACT

Captive *Pterocles namaqua* and *P. bicinctus* showed behavioural adaptations for thermoregulation and water conservation. Reduction of environmental and metabolic heat loads by day, and conservation of metabolic heat at night, were achieved by altering activity levels and by exploiting or creating appropriate microclimatic conditions. Experimental dehydration and field observations indicate that *P. namaqua* drinks only every 3-5 days normally, and that both species can easily withstand such water deprivation by augmenting water conservation measures. Birds were gregarious, but social interactions were pacific, undemonstrative and egalitarian.

reported here, and are used to interpret behaviour of birds seen in the field.

2 MATERIALS AND METHODS

The study was performed in Namibia in January–February 1980, based mainly at the Namib Desert Research Station, Gobabeb (23°34'S, 15°03'E) with supplementary field observations in the Namib Desert around Ganab (23°06'S, 15°33'E) and Zebra Pan (23°31'S, 15°28'E) and in the Etosha National Park in the vicinity of Okaukuejo (19°10'S, 15°55'E). In both the Namib and Etosha areas Namaqua sand-grouse (*Pterocles namaqua* (Gmelin)) and double-banded sand-grouse (*P. bicolinctus* Temminck) were the common sand-grouse species. Specimens of both species were caught under licence by mist-netting beside artificial water-holes in the Namib Desert. Three male and four female *P. namaqua* were caught during morning drinking flights at Zebra Pan and transferred to the aviary at Gobabeb the same morning. Four *P. bicolinctus* (two of each sex) were caught during their evening drinking flights at Ganab and transferred to the aviary the following morning. On arrival at Gobabeb, all birds were weighed and marked individually with different colours of nail varnish on bill and feet before release into the aviary; these marks allowed individual recognition in daylight without recapture.

Aviary dimensions were 6,3×3,2×8 m (L×W×H); it was made of chicken wire on a pipework frame, built on the natural substrate of sandy gravel. The availability of shade depended on the time of the day: complete shade from adjacent buildings lasted until 09h45 (local solar time, LST: see below); wooden slats over one quarter of the roof provided 35% shade until 14h30 LST; after 14h30 LST partial shade was still available from the cage framework and from the chicken wire where it was at an oblique angle to the sunlight. In the absence of early morning fog, some direct sunlight was available at all times from somewhat before 07h00 LST.

Air temperatures 5 cm above the ground at three chosen points in the aviary were measured with thermistors, shaded from direct sunlight using expanded polystyrene cups lying on their sides to allow circulation of air. Thermistors were connected via long leads to a YSI telethermometer in a building immediately beside the aviary, whence all observations of bird behaviour were made. By noting whether thermistors were in complete, partial or no shade, estimates of air temperature differences between these conditions could be made. In addition, a selection of weather data for the relevant period was abstracted from the records of a first order weather station and a recording solarimeter, both sited within 100 m of the aviary. All weather and behaviour records were made at local civil time (S. African Standard Time = GMT + 2h) but converted to local solar time (LST = GMT + 1h) for publication, since solar time is biologic-

ally the more relevant measure; thus sunrise and sunset are symmetrically disposed about 12h00 LST, the time of the solar zenith when maximum potential solar irradiance will occur.

Birds were fed a commercial cage bird (budgerigar) seed mixture *ad libitum*, which they foraged from the ground. Tap water was available *ad libitum* from plastic bowls sunk in the ground, except for a 3-day experimental dehydration period. Observations were made on birds with free access to water during 31 January to 7 February. At 16h00 – 17h00 LST on 7 February birds were caught and held overnight in darkened boxes without water, weighed the following morning in a post-absorptive state and returned to the aviary (whence water had been removed) between 09h30 and 11h30 LST. Birds then had no water from 8–10 February inclusive; on 11 February they were recaptured at 05h30 – 05h50 (i.e. before they had started to feed) and held in darkened boxes. One at a time, the birds were then weighed, returned to the aviary, watched until they drank at the restored water supply (when the number of sips was counted) and then recaptured and reweighed. Weight losses and gains were calculated for dehydration and rehydration phases. This protocol exposed birds to dehydration for not less than 96–99h (depending on the individuals), of which 2,5 days were spent exposed to full sunlight.

From an immediately adjacent building, windows (covered except for observation slits, to minimise disturbance) gave an uninterrupted view of birds in the aviary. In addition to descriptive notes made as behaviour occurred, the following numerical data were recorded at intervals (15 – 30 – 60 min) through the day time; thermistor temperatures; the number of birds (separately by species) involved in each of the following activities: sitting, standing, walking, preening, being in shady as opposed to sunny positions, feeding, drinking, huddling (i.e. being stationary and in contact with at least one neighbouring bird), having dorsal (mantle) feathers erect, gular fluttering, and holding wings drooped and away from the sides (wing drooping) (cf. Dixon & Louw's (1978) Fig. 4).

In order to make these data comparable between species, the number of birds of each species carrying out an activity on a given occasion was expressed as a proportion of the birds so involved, by dividing the number by the total number of individuals of the same species. Mean proportions were calculated for each hour of the day (i.e. from 00 to 59 minutes past each hour), using observations on all relevant days to build up a generalised picture of daily activity patterns, but keeping data separate between species and between periods when water was and was not available to enable estimation of interspecific differences and of the effects of dehydration within species.

The statistical validity of dehydration effects and of interspecific differences was tested by means of paired *t*-tests, using serial contemporaneous pairs of mean proportions. Where no significant difference was found

between two series of means, the data were combined and a joint mean for each hour was calculated and plotted. All means are given \pm their standard errors, with the number of observations in parenthesis. The number of degrees of freedom (d.f.) are shown as t(d.f.) for t-tests.

3 RESULTS

3.1 Weather and the aviary microclimate

Relevant weather station data are shown in Table 1; the weather during periods of observation of hydrated and dehydrated birds was essentially similar, except that the former period experienced higher air temperatures and lower solar irradiance than the latter. This difference in air temperatures between periods was also found in the aviary: Figure 1 shows air temperatures under conditions (sun or shade) chosen by most birds at any given time through the day. In the aviary, average air temperature differences measured between thermistors in sun and full or partial shade were $5,2 \pm 0,4^\circ\text{C}$ (9) and $3,8 \pm 0,2^\circ\text{C}$ (47) respectively. Inspection of traces from the solarimeter and screen thermograph showed that insolation peaked almost symmetrically at 12h00 LST (consistent with generally cloudless conditions, at least after mid-morning, on most days) while air temperatures reached maxima between 14 and 15h LST, as is commonly observed and is shown in Figure 1.

3.2 Body weights

At capture, the mean body weight of *P. namaqua* ($168,0 \pm 3,5$ g (7)) was significantly lighter ($t(10) = 2,86$; $P < 0,02$) than that of *P. bicinctus* ($189,1 \pm 6,5$ g (4)). During the observation period following capture (when the birds were hydrated), many lost but some gained weight,

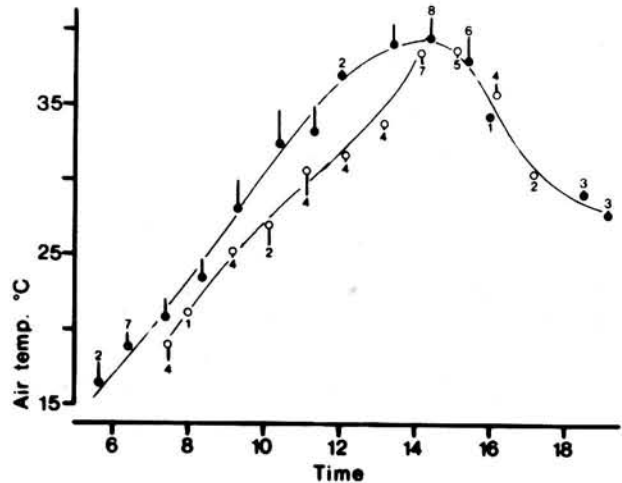


FIGURE 1: Air temperature 5 cm above the ground in the aviary, in conditions of sun, full or partial shade occupied by most birds at the time. Points show mean air temperatures in each hour at the mean local solar time of observations. Filled and open symbols represent means during periods when birds were hydrated ($n=2-11$) and dehydrated ($n=1-7$) respectively, and bars represent standard errors of the means. For all times and some temperatures, the plotting symbol is larger than the SEM bar would be.

TABLE 1: Selected data from the Gobabeb weather station (mean \pm SEM (range)) for the periods 31 January – 7 February and 8–10 February 1980, corresponding to periods of observations of behaviour of hydrated and dehydrated sand-grouse respectively. Comparisons between periods by t-test.

PARAMETER	31 JAN. – 7 FEB. (HYDRATED BIRDS)	8–10 FEB. (DEHYDRATED BIRDS)	P < (df = 9)
TEMPERATURE, $^\circ\text{C}$:			
Screen, minimum	$16,7 \pm 0,9$ (14,3 – 20,8)	$11,8 \pm 0,7$ (10,7 – 13,1)	0,002
Screen, maximum	$32,0 \pm 1,1$ (27,4 – 36,1)	$28,5 \pm 0,7$ (27,4 – 29,9)	0,05
Screen, 13h00 LST	$30,5 \pm 1,3$ (24,5 – 34,6)	$26,6 \pm 0,6$ (25,5 – 27,2)	0,02
Soil surface, 07h00 LST		$19,7 \pm 1,0$ (14,0 – 25,0)*	
Soil surface, 13h00 LST		$55,6 \pm 0,8$ (50,0 – 59,2)*	
RELATIVE HUMIDITY, %:			
Screen, 07h00 LST		80 ± 5 (43–95)*	
13h00 LST		35 ± 2 (27–46)*	
19h00 LST		37 ± 3 (25–61)*	
WIND RUN, km/day:		153 ± 5 (126–177)*	
SOLAR IRRADIANCE:**			
Total, J/m^2 day, mean	$(2,36 \pm 0,04) \times 10^7$	$(2,51 \pm 0,03) \times 10^7$	0,02
range	$(2,19-2,47) \times 10^7$	$(2,45-2,56) \times 10^7$	0,02
Maximum, W/m^2		906 ± 8 (872–956)*	
Time of maximum		12h00 \pm 0*	

*A combined mean ($n=11$) etc. is shown in the absence of a significant difference between periods.

**Short-wave = visible + near infra-red.

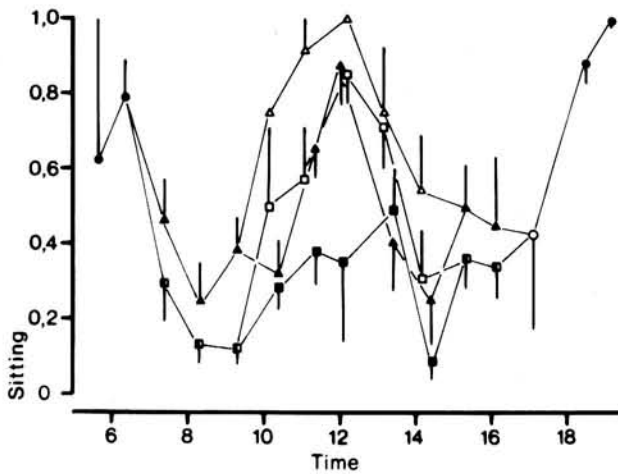


FIGURE 2: The proportions of *Pteocles namaqua* (squares) and *P. bicinctus* (triangles) sitting at different times of day (local solar time, LST). Birds were either hydrated (filled symbols) or dehydrated (open symbols). Species and/or hydration levels are shown separately only when a series of points were significantly different by the paired t-test. Points representing a combination of species or treatments are shown by circles or partially filled symbols respectively. Points and bars represent means and one standard error of the mean respectively. The number of observations for each mean (n) was 2–15. See text for further details of calculations etc. Results of paired t-tests for series of points plotted separately are as follows: Interspecific differences: hydrated birds, $t(9) = 3,23$; $P < 0,02$; dehydrated birds, $t(9) = 4,97$; $P < 0,001$. Intraspecific effects of dehydration: *P. namaqua*, $t(4) = 5,35$; $P < 0,01$; *P. bicinctus*, $t(4) = 5,79$; $P < 0,01$.

and the mean weight changes (*P. namaqua*: $-0,62 \pm 0,29$ (7)); *P. bicinctus*: $-0,41 \pm 0,36$ g/100 g body weight/day (4)) were not significantly different from zero. This is consistent with observations that birds learnt quickly to feed and drink in the aviary, and that they appeared to be able to find and would eat all types of seeds in the mixture provided. Weight losses on dehydration were not significantly different between species (*P. namaqua*: $3,4 \pm 0,4$ (7); *P. bicinctus*: $4,4 \pm 0,2$ (4) g/100 g BW/day (4)).

3.3 Stance and ambulatory activity

The daily patterns of sitting, standing and walking (mutually exclusive activities) are shown in Figures 2, 3 and 4 respectively. All birds sat in tight huddles overnight (see section 3.4.2); thus birds were usually found at or before sunrise sitting in the same place as they had been seen last, 1–2h after the previous sunset. By day, activity patterns were polymodal: in general, proportions of birds sitting peaked early and late in the day and about the solar zenith, while proportions of birds standing and walking peaked mid-morning and mid-afternoon. However, midday peaks or troughs were not marked in hydrated *P. namaqua*.

Interspecific differences and effects of dehydration were apparent only during the main part of the day. In

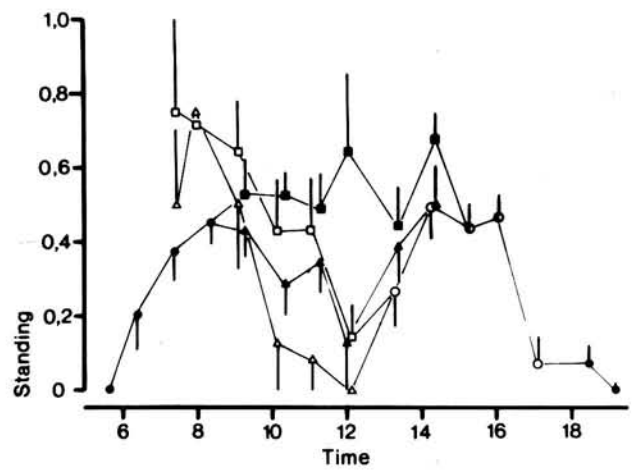


FIGURE 3: The proportions of *Pterocles namaqua* (squares), *P. bicinctus* (triangles) standing at different times of day (local solar time). Birds were either hydrated (filled symbols) or dehydrated (open symbols). Points representing combination of species or treatments are shown by circles or partially filled symbols respectively; $n=2-24$. See Fig. 2 for other details. Results of paired t-tests are as follows. Interspecific differences: hydrated birds, $t(5) = 3,05$; $P < 0,05$; dehydrated birds, $t(5) = 3,38$; $P < 0,02$. Intraspecific effects of dehydration (10–15h only): *P. namaqua*, $t(4) = 2,45$; $0,10 < P < 0,05$; *P. bicinctus*, $t(4) = 4,12$; $P < 0,02$.

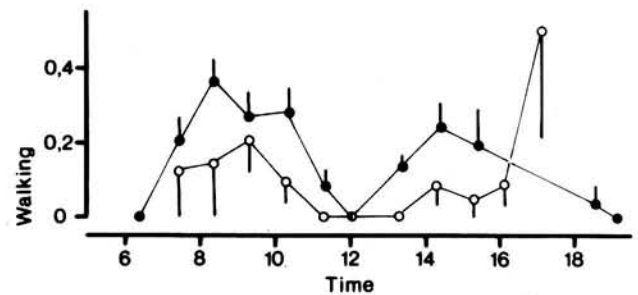


FIGURE 4: The proportions of both sand-grouse species walking at different times of day (local solar time). Birds were either hydrated (filled circles) or dehydrated (open circles); $n=4-24$; see Fig. 2 for other details. Results of paired t-tests are as follows: There were no significant interspecific differences and data for both species were combined. Effects of dehydration: $t(9) = 5,28$; $P < 0,001$.

general, *P. bicinctus* were less active than *P. namaqua* (i.e. greater proportions sitting and lesser standing). Although proportions of the two species walking were similar at any time, *P. bicinctus* walked slowly and circumspectly, while *P. namaqua* walked more quickly and with a “busy” manner. Dehydration increased general inactivity in both species: lesser proportions stood or walked and greater proportions sat than when hydrated. In addition, dehydrated birds seemed to spend more time asleep during the day, but quantitative data are lacking.

3.4 Thermoregulatory behaviour

This section deals with certain aspects of behaviour (illustrated in Figure 5) which can be related primarily to

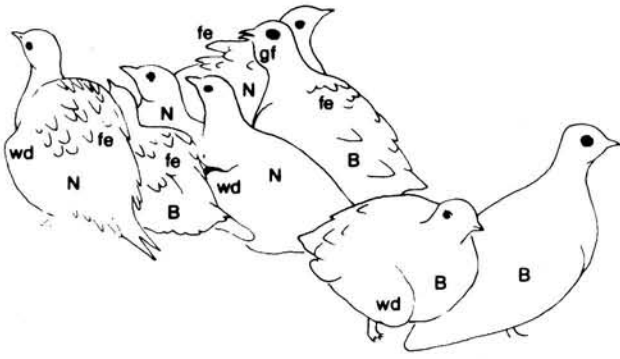


FIGURE 5: Tracing from a photograph (taken at 13h25 local solar time) of hydrated captive sand-grouse (*Pterocles namaqua* (N) and *P. bicinctus* (B)), to illustrate several aspects of thermoregulatory behaviour. The upper left group were in a typical daytime huddle in partial shade: some sitting, others standing (not seen in night-time huddles), not very closely packed and mostly facing the sun. The two right-hand birds were in somewhat more extensive shade than the others. Gular fluttering (gf), feather erection (fe) and wing drooping (wd) can all be seen, although not all in any single bird.

the control of heat exchange between the birds and their environment. Using the proportions of birds involved as an indicator of relative importance, choice of shade (Figure 6), huddling with other birds (Figure 7), and erection of dorsal feathers (Figure 8) are apparently the principal mechanisms used by non-incubating birds, while wing drooping and forced evaporation by gular fluttering (Figure 9) seem less important in maintaining heat balance. The birds' state of hydration had significant effects on all these behavioural mechanisms, but differential response between species could be detected only for feather erection.

Evidence to be presented elsewhere (Thomas & Maclean, in preparation) suggests that *P. namaqua* and *P. bicinctus* maintained rather constant daytime deep body (colon) temperatures in the range 40–42°C even at ambient air temperatures of 45–50°C. Night-time deep body temperatures were somewhat lower.

3.4.1 Choice of shade vs. sun

Captive birds chose to sit in the sun (if available) early in the morning, but would almost all be in shade from solar zenith and through the afternoon period of maximum air temperatures (Figure 6). Dehydration accentuated these effects. Birds basking in the morning tended to stand broadside on to sunlight, while birds in partial shade during the heat of the day tended to face towards (or occasionally directly away from) the sun (Figure 5). Evidence that active selection was involved derives from frequent observations that birds would congregate in a disproportionately small area of sun or shade (depending on circumstances), and would move with this patch of sunlight or shadow.

We obtained corresponding field observations of *P. namaqua* foraging in sunlight in the morning, and sitting

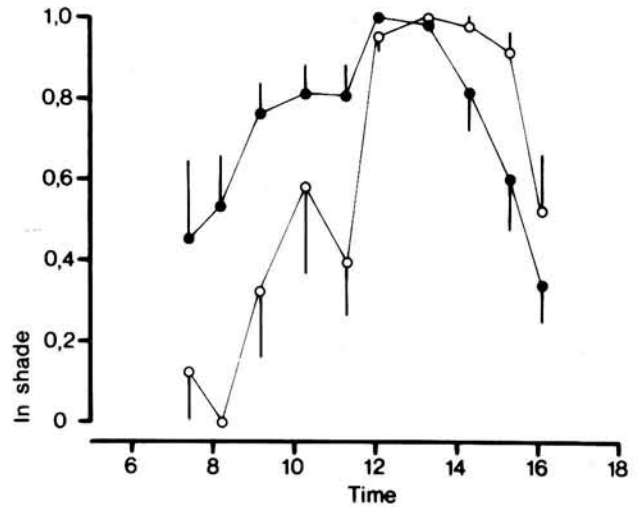


FIGURE 6: The proportions of both sand-grouse species choosing shade at different times of day (local solar time) plotted only for times when the choice of sun vs. shade was available. Birds were either hydrated (filled circles) or dehydrated (open circles); $n=2-19$; see Fig. 2 for other details. Results of paired t-tests are as follows: There were no significant interspecific differences and data for both species were combined. Effects of dehydration: before 12h00 LST, $t(4) = 7.52$; $P < 0.002$; after 14h00, $t(2) = 4.75$; $P < 0.05$.

in shade during the early afternoon period of maximum air temperatures.

3.4.2 Huddling behaviour

Huddling in groups of up to seven birds was the normal situation overnight, and recurred during the heat of the day, especially amongst dehydrated birds (Figure 7). Such behaviour would be extremely difficult to see in the wild, because the immediate response to disturbance was for individuals to leave the huddle and crouch again having separated by a few metres from one another.

There were differences between day and night-time huddles. At night birds sat invariably with bellies on the ground and tightly packed against one another. Nocturnal huddles were often beside a small bush or large stone, and were started by a single bird forming a scrape, rocking from side to side on its belly, rotating and wriggling, and kicking material out behind. Second and subsequent birds snuggled up to the others or interpolated themselves between birds already huddled side by side, during a period of fidgeting and rearrangement lasting 10–15 min, when middle positions appeared to be preferred over end ones. Namaqua sand-grouse had a strong preference for having adjacent birds facing alternate ways at night: the ratio of numbers of adjacent pairs of birds sitting in parallel to the numbers sitting in antiparallel arrangement was 11:30. The probability (P) of such an arrangement occurring by chance is 0.0014 (Binomial equation). In contrast, *P. bicinctus* showed no apparent preference, with a ratio of parallel: antiparallel arrangement of 10:11 and $P=0.168$.

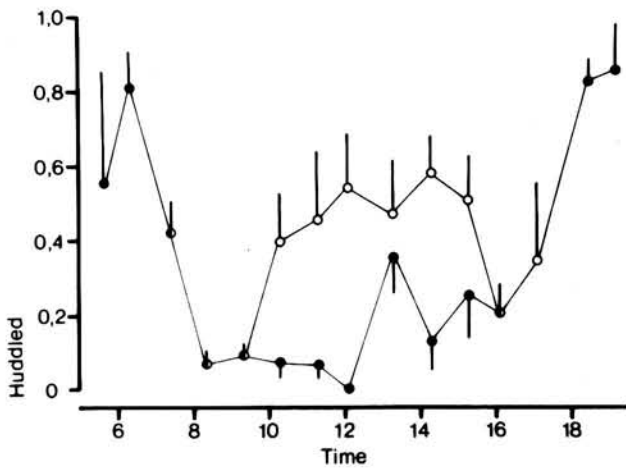


FIGURE 7: The proportions of both sand-grouse species huddled together at different times of day (local solar time). Birds were either hydrated (filled circles) or dehydrated (open circles); $n=2-25$; see Fig. 2 for other details. Results of paired t-tests are as follows: There were no significant interspecific differences and data for both species were combined. Effects of dehydration: $t(5) = 5,69$; $P < 0,01$.

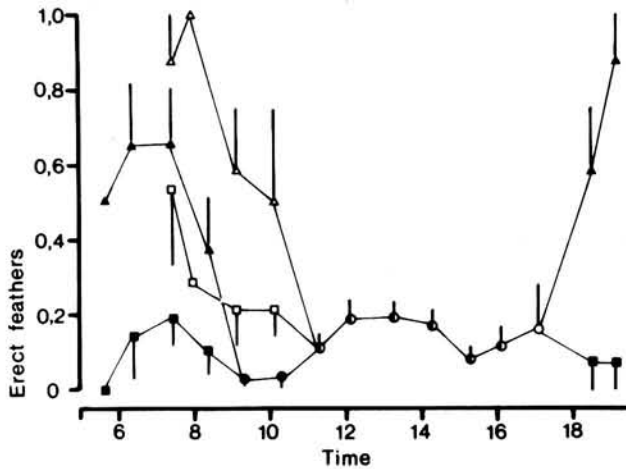


FIGURE 8: The proportions of *Pterocles namaqua* (squares) and *P. bicinctus* (triangles) with erect dorsal feathers at different times of day (local solar time). Birds were either hydrated (filled symbols) or dehydrated (open symbols). Points representing combinations of species or treatments are shown by circles or partially filled symbols respectively; $n=2-29$; see Fig. 2 for other details. Results of paired t-tests are as follows: Interspecific differences; hydrated birds, $t(5) = 7,27$; $P < 0,001$; dehydrated birds, $t(3) = 4,39$; $P < 0,05$. Intra-specific effects of dehydration: *P. namaqua*, $t(3) = 4,87$; $P < 0,02$; *P. bicinctus*, $t(3) = 5,35$; $P < 0,02$.

Daytime huddles differed in having birds both standing and sitting, in the absence of scrape formation, and in being less tightly packed together, although middle positions still seemed at a premium. There was still no preference for parallel or antiparallel arrangement by *P. bicinctus*, but in *P. namaqua* the night-time preference was reversed and now they showed a strong preference for parallel orientation (parallel : antiparallel = 44:26; $P=0,0095$), which may have arisen from the birds' strong tendency to face the sun.

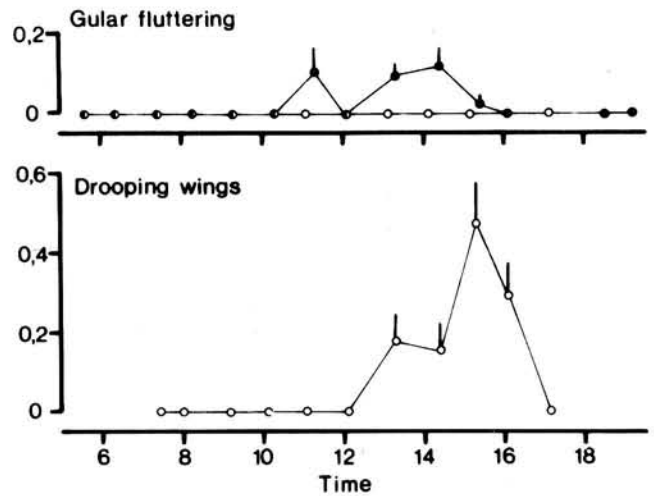


FIGURE 9: The proportions of both sand-grouse species showing gular fluttering (above; $n=4-26$) and drooping wings (below; $n=4-12$) at different times of day (local solar time). Wing drooping was not recorded systematically during the hydration period, during which it was not a conspicuous feature of behaviour. Birds were either hydrated (filled circles) or dehydrated (open circles); see Fig. 2 for other details. There were no significant interspecific differences (paired t-test) and data for both species were combined. Effects of dehydration on gular fluttering: $t(4) = 2,89$; $P < 0,05$.

3.4.3 Feather erection

Feather erection was comparatively unimportant during the heat of the day, but was more so in the mornings and evenings, when feather posture was differentially affected both by dehydration and between species (Figure 8).

3.4.4 Gular fluttering and drooping wings

Gular fluttering was not used much by captive sand-grouse when hydrated and not at all when dehydrated (Figure 9). In comparison, an incubating female *namaqua* watched one day near Ganab spent $28 \pm 6\%$ (5) of her time gular fluttering between 11h30 and 14h30 (LST), at ambient temperatures of $40,9 \pm 0,2^\circ\text{C}$ (5) 5 cm above the ground.

Wing drooping was not common amongst hydrated birds, and was not recorded systematically until it became obvious after birds were dehydrated. In such birds, it was clearly associated with times of high ambient temperature (Figure 9).

3.5 Feeding and drinking

Feeding and drinking by captive birds occurred mainly morning and afternoon with minimal activity around solar zenith, although this pattern was not very marked (Figure 10). Feeding bouts for any individual were typic-

ally short, interspersed between relatively prolonged periods of other activities. Foraging behaviour was distinctly different between species: *P. namaqua* usually fed while walking along, with only brief halts, whereas *P. bicinctus* had longer pauses and apparently made a more thorough search with more pecks at each halt. The extra time (i.e. higher proportion of birds at any time: see Figure 10) spent feeding by hydrated *P. bicinctus* compared to *P. namaqua* may be correlated with the slower movements of the former species (see section 3.3).

Individual birds took only 1–4 sips at a time, but might return to drink at several times during the day. Both species therefore took advantage of the constant proximity of water to drink at atypical times of day. Despite the possible stimulus and synchronising effects of flocks of wild *P. namaqua* flying over the aviary to drink at a pool nearby, captive *P. namaqua* failed to show sharp peaks of drinking in early morning and late afternoon. On the other hand, despite drinking during the day (which wild *P. bicinctus* never do) this species showed a remarkable conservation of their normal evening drinking behaviour (Figure 10) without any synchronising effect from wild *P. bicinctus*, which did not occur around Gobabeb at the time of these studies. Captive *P. bicinctus* formed typical night-time huddles at or soon after sunset (about 18h30 LST), but dispersed again about 19h00 and made their way to the water bowls by 19h15, precisely when the main drinking flocks of wild *P. bicinctus* arrived at the Ganab water-hole (about 70 km away) where captive birds had been netted. This behaviour was repeated night after night (even when bowls were empty during the dehydration experiment), but *P. namaqua* were not stimulated to follow. Having visited the water bowls, *P. bicinctus* reformed their huddle.

Dehydration for 3 days was survived easily. On regaining access to water, *P. namaqua* drank $8,0 \pm 0,5$ (7) g $H_2O/100$ g BW (77% of mean total weight loss during the dehydration period) which was significantly less ($t(10) = 4,45$; $P < 0,002$) than the $12,0 \pm 1,0$ (4) g/100 g BW drunk by *P. bicinctus* (98% of mean total weight loss). The water intake per sip was not significantly different between species, and the mean for all birds was $2,34 \pm 0,24$ (11) g water/sip. Wild *P. namaqua* drank 8–10 sips before leaving the water-hole, equivalent to 18,7 – 23,4 g H_2O or 11,1 – 13,9% body weight. Dehydration depressed feeding activity in *P. bicinctus* but not in *P. namaqua*.

3.6 Comfort movements

Birds preened at all times of day, although significantly more commonly in the forenoon (mean proportion of birds = $0,105 \pm 0,017$ (95)) than in the afternoon ($0,050 \pm 0,010$ (140); $t = 2,80$; $P < 0,01$).

Stretching was also common. The two most usual movements maintained low silhouettes and presumably aid

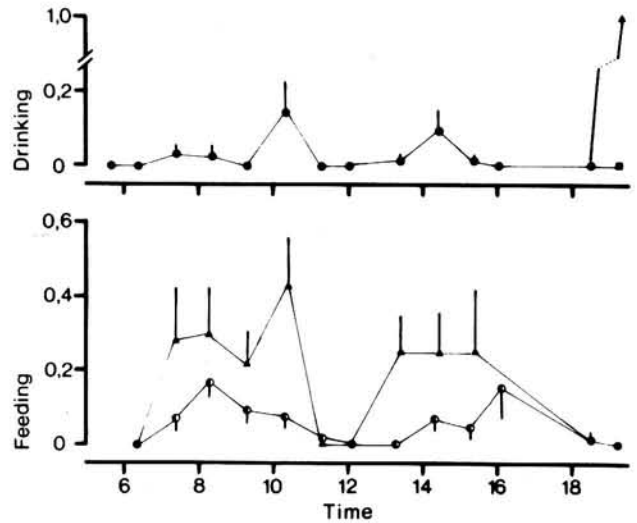


FIGURE 10: The proportions of *Pterocles namaqua* (squares) and *P. bicinctus* (triangles) drinking (above; $n=3-23$) and feeding (below; $n=3-20$) at different times of day (local solar time). Birds were hydrated (filled symbols) or dehydrated (open symbols). Points representing combinations of species or treatments are shown by circles or partially filled symbols respectively; see Fig. 2 for other details. No significant interspecific differences in drinking behaviour were demonstrable except at 19h15. No significant differences in feeding behaviour were demonstrable between hydrated and dehydrated *P. namaqua*, or between dehydrated *P. namaqua* and *P. bicinctus*, and these data were combined (part-filled circles, lower graph). Effect of dehydration on *P. bicinctus*: $t(8) = 4,26$; $P < 0,01$.

crispis: in the first, a standing or walking bird would tip forward onto its breast/belly and stretch one or both wings up over its back, while keeping elbow and wrist joints bent, then either remain sitting, or stand up and continue its former activity; in the second form, a sitting bird would roll on its side, stretch the upper wing over its back (i.e. approximately parallel to the ground) and also usually stretch out its legs. A less common pattern involved a standing bird stretching legs, body, neck, head and wings upwards; this created a much more conspicuous silhouette than the other movements.

Sand bathing was seen occasionally.

3.7 Social behaviour

Birds were gregarious, constantly forming groups even when not huddled and not constrained to a small area by choice of shade or sun. Namaqua sand-grouse responded positively to flocks of wild conspecifics overhead (by pacing, showing flight intention movements and flying up), but *P. bicinctus* did not respond to these flocks. Amongst captive birds, there was a general tendency for conspecifics to associate, although mixed species groupings also occurred.

Birds were pacific and egalitarian, yielding place freely to one another, even when jockeying for prime positions in huddles. No evidence was found for aggressive, dominating or hierarchical behaviour between in-

dividuals, nor were positive or negative associations apparent between particular birds.

Movements and behaviour patterns appeared strictly functional and lacked ritualisation or signalling value as such, with the single exception of flight intention movements.

4 DISCUSSION

The relevance of observations on captive birds to their behaviour in the wild must be an important consideration when assessing the present results. Certainly the permanent proximity of water was an artificial aspect of the captive environment, and the relatively high density of seeds may also have been so, although patchy plant distribution and particle assortment by the wind can result naturally in local concentrations of seeds. Disturbance due to human activities was presumably unnaturally high: although people were normally out of sight, background noises were sometimes obtrusive. These intermittent disturbances can be considered equivalent (in some respects) to disturbance by predators in the wild (which is not infrequent as shown by field observations), and there were certainly times and days when human disturbance was slight.

Several points favour the view that the present observations may be a reasonable approximation to a knowledge of natural behaviour. Firstly, birds settled well in captivity, feeding and drinking readily so that weight losses were small, and apparently habituating soon to many of the unnatural disturbances. Secondly, since observations were on wild-caught birds within 2 weeks of capture, there was no opportunity for selection of traits for captivity, and little opportunity for learnt abnormalities of behaviour. Thirdly, many behavioural patterns seen in captivity may be matched with similar observations in the wild, or can be shown to be adaptive to the natural environment (see below).

A major feature in favour of this study is that it is difficult or impossible (because of the open nature of the habitat) to obtain a regular series of co-ordinated observations on free sand-grouse away from water-holes or nests without their being aware of the observer's presence. By contrast it is reasonably sure that our captive birds were usually unaware of surveillance, in that periods of observations could be started without the birds showing signs of special alertness or anxiety such as characterised responses to disturbance.

4.1 Behavioural responses to the thermal environment

Many of the behavioural patterns reported may be rationalised in terms of their thermoregulatory significance. This is not surprising, since the natural environment of sand-grouse is a rather extreme one in thermal terms.

Calculation of heat exchange between real animals and their environment is complicated by geometrical considerations. However, it is illuminating to consider heat fluxes near the ground quantitatively as far as possible, to indicate the relative importance of different components which determine the heat balance of an animal.

It is convenient to consider short-wave (visible and near infra-red) and long-wave (far-IR) radiation separately. Potentially, solar radiation comprises the biggest radiative component: mean downward short-wave radiation varied between zero and 906 W/m^2 (Table 1), to which must be added a downward solar long-wave component (approximately 30% of short-wave = 0 to 272 W/m^2 : (Gates, 1962)) and (for purposes of an animal's heat load) an upward component of short-wave radiation reflected from the ground. Since the reflectivity to short-wave radiation (0,35 – 0,60 for dry sand: (Lowry, 1969)) decreases with increasing solar altitude, the reflected solar short-wave component may be quite high for large parts of the day (e.g. $0,35 \times 906 = 317 \text{ W/m}^2$ at 12h00 LST; $0,6 \times 300 = 180 \text{ W/m}^2$ at about 07h00 and 17h00. Reflected long-wave fluxes can be neglected generally, because most materials have very low reflectivities (0,05) at these wave-lengths (Birkebak, 1966).

Emission of long-wave radiation occurs from all matter at temperatures above zero K as described by the Stefan-Boltzmann (fourth power) law. Thus, there is an exchange of long-wave radiation between an animal, its solid (and liquid) surroundings and the atmosphere. The net value and direction of any exchange depends on the relative temperatures and emissivities (= (1–reflectivity), usually 0,95 in the far-IR) of the radiant surfaces. The mean radiant temperatures of a clear atmosphere is 263K, but only about 60% of far-IR reaches the ground because of absorption by CO_2 and water vapour (Gates, 1962): near sea level, this downward component is approximately 160 W/m^2 . The range of radiant surface temperatures experienced by our sand-grouse can be taken as of the same order as the soil surface temperatures in Table 1, although there are several reasons for supposing that values for radiant temperatures would have varied beyond the range by some degrees in both directions. At these temperatures there could be net long-wave radiant losses from solids to the atmosphere of the order of 200 to 500 W/m^2 , and net exchanges between solids of ± 5 to $7 \text{ W/m}^2 \cdot ^\circ\text{C}$ depending on the absolute temperature and temperature differences. Thus, radiant energy exchange is dominated by the solar components during the day and by losses to the atmosphere (especially if clear) at night.

Conductive and convective heat exchanges are highly dependent on the geometry of the body concerned, and order-of-magnitude calculations have been done for a cylinder of approximately sand-grouse dimensions (0,15 m long \times 0,07 m diameter). For forced convection parallel to the cylinder's long axis at the average wind speed experienced (1,77 m/s: Table 1), calculated heat exchange would have been $15,7 \text{ W/m}^2 \cdot ^\circ\text{C}$ for each

degree difference between surface and air temperatures (Calder and King, 1974). The thermal conductivity coefficient of feathers was assumed to be similar to fur, and as calculated as $4.43 \times 10^{-5} \text{ W/m}^2 \text{ }^\circ\text{C}$ from data in Birkebak's (1966, Figure 19). Conductive heat transfer per degree Celsius temperature difference across the feather layer was calculated as about $8.2 \times 10^{-3} \text{ W/m}^2$ (0.5 cm insulative thickness) or $3.9 \times 10^{-3} \text{ W/m}^2$ (1.0 cm insulative thickness).

The metabolic rate for *P. namaqua* and *P. bicinctus* at rest (calculated from body weights, using standard allometric equations for non-passerines: Calder and King, 1974) comes to 1.2 to 1.3 W/bird or about 49 W/m² external surface (Walsberg and King, 1978). It is known that many desert animals have metabolic rates less than expected on the basis of standard allometric equations, but nothing is known about sand-grouse in this respect. Various activities augment metabolic rates above basal levels (Wunder, 1975): for example, Redshanks (*Tringa totanus*) standing alert or foraging increase their metabolic rates by about 30% or 100% respectively over rates when asleep (Ferns, Macalpine-Leny and Goss-Custard, 1979). Approximately 75% of metabolic energy is released as heat, while 15–350% of metabolic heat production may be dispersed as latent heat of evaporation of body water (2.43 kJ/gH₂O) depending on species and ambient temperatures (Calder and King, 1974).

The geometry of the system is the main difficulty in integrating the effects of all these potential exchanges of heat on an animal's heat balance: different surface areas and orientations are involved for the different components. However, one can see from the foregoing data that, for sand-grouse in their natural environment, heat loads during the day could be minimised by avoiding direct and reflected sunlight while maintaining exposure to a clear sky (for radiant heat loss), by having solid surroundings at or below (rather than above) body temperatures, and by reducing metabolic heat production. Forced convection can be a potent means of dispersing heat if bare skin can be exposed to a cool wind, since skin temperatures can be raised to near deep body temperatures by increasing cutaneous blood flow. At night, heat losses can be minimised by reducing surface areas exposed to the sky (especially if clear) and by having solid surroundings as near as possible to body temperatures. At all times, insulation is a potent mechanism for retarding heat transfer when temperature gradients would otherwise lead to unfavourable heat gain or loss by the animal. In fact, our observations show that both *P. namaqua* and *P. bicinctus* behaved much as expected if they were to minimise heat loss during the colder periods and heat gain during the hotter periods of the 24-hour cycle.

Many daytime behaviour patterns can be interpreted as mechanisms likely to reduce or disperse the total heat load during the hottest period: relative inactivity to reduce metabolic heat production; choice of shade to

minimise solar radiant heat load and to experience lower air temperatures; huddling to provide an immediate environment with more equable surface and deep temperatures than those of the general environment; gular fluttering by hydrated birds to disperse heat; erection of dorsal feathers to insulate the skin mainly from high outer surface temperatures (not so much from high air temperatures since generally these did not exceed deep body temperatures: Figure 1). These activity patterns were clearly in register with either the pattern of solar radiation (i.e. peaks or troughs about noon: sitting, standing, walking, feeding, drinking, and choice of shade by hydrated birds) or that of ambient temperatures (i.e. peaks at 14–15h LST: huddling by hydrated birds, wing drooping) or had peaks spanning both insolation and temperature maxima (choice of shade and huddling by dehydrated birds, feather erection and gular fluttering). Individual birds adopted a mixture of these thermoregulatory mechanisms which was not necessarily consistent within the group at the time nor from time to time, nor was any individual seen to use all available mechanisms at once. The latter suggests that *P. namaqua* and *P. bicinctus* had thermoregulatory reserves and could readily withstand larger heat loads than obtained during our observations.

Since wing drooping occurred characteristically during the heat of the day, one may assume that it is mainly a means of heat dispersal, although it is not obvious *a priori* whether it would result in net gain or loss of heat, because the lightly insulated axillary region might experience increased radiant heat gain (reflected short-wave + long-wave if soil surface temperature exceeds skin temperature), or it might experience increased convective heat loss if skin temperature exceeds air temperature. It seems likely that the relatively narrow gap between body and wings (which we never saw as wide in non-incubating birds as indicated in Dixon and Louw's (1978) figure 4 of an incubating bird) results in the axilla being shaded from much of the potential radiant heat load but allows passage of wind through the gap and hence heat loss by forced convection. Indeed, since fluid flowing through a constriction accelerates (the Venturi principle) and since forced convective heat exchange is proportional to (wind velocity)^{0.5}, wing drooping may actually enhance convective heat loss above the level expected for the mean wind velocity. It is possible that the prevalence of wing drooping during the period of dehydration may have been only coincidental, and that the significant factor over this period was the lower air temperatures (associated with cooler westerly winds from the Atlantic; Table 1) which would have made convective heat loss more effective. It is probably significant that wing drooping by several N. African sand-grouse species (*P. coronatus*, *P. senegallus*, *P. lichtensteini*, *P. alchata* or *P. orientalis*) was never observed (Thomas and Robin, 1977); these species were exposed to air temperatures above likely body temperatures (40°C) for several hours per day, which would result in convective heat gain by the birds.

There seems little doubt that these apparently thermoregulatory behaviour patterns are available to and are used by sand-grouse in the wild. Even in the Namib Desert small bushes, grass tussocks and large stones provide shade; vegetation is much more readily available over much of the range of both *P. namaqua* and *P. bicinctus* (Snow 1978), and shade is used by these and other species (this study; George, 1969). However, some mechanisms (such as choice of shade and huddling) which seem important to birds without nests are not available to incubating birds. Thomas and Robin (1977) and Dixon and Louw (1978) emphasised the importance of feather erection, gular fluttering and (in *P. namaqua* but not *P. alchata*, *P. coronatus* or *P. senegallus*) wing drooping and orientation by incubating females, and it may be that these mechanisms become relatively more important while birds are necessarily solitary and exposed on a nest.

Although hitherto unreported in sand-grouse, nocturnal huddling is well-known in many bird species, providing a local environment close to body temperatures, and reducing the surface area exposed to the night sky, the major heat sink. Radiant heat loss to the sky would also have been reduced by the habit *P. namaqua* and *P. bicinctus* had of huddling close to a bush or stone, with the additional advantage of camouflage by breaking the birds' silhouettes. Ward (1972) and Ward and Zahavi (1973) state that sand-grouse roost solitarily, rationalising that communal roosts would be vulnerable to predators. Our observations suggest that both these statements are incorrect with respect to *P. namaqua* and *P. bicinctus*; moreover the absence of field observations of huddling (night or day) by these or other sand-grouse species cannot be taken as evidence that huddling does not occur, since our observations show that huddles break apart on disturbance and so would be unlikely to be seen in the wild. It seems likely that, in addition to heat conservation, an advantage of roosting in a huddle would be to reduce vulnerability by group vigilance, enhanced by the possibility of communicating alertness within the group by tactile (silent) means.

Thus, behavioural mechanisms of thermoregulation by *P. namaqua* and *P. bicinctus* seem very important, often bringing to mind similar behaviour by heliothermic reptiles. One benefit of such an astute use of small scale variations in microclimate would be conservation of energy (and water), which would help to explain the relative success of sand-grouse in biologically unproductive environments.

4.2 Responses to dehydration

Namaqua and double-banded sand-grouse are evidently well adapted to dehydration, easily surviving 3 days' exposure to a normal environment without water. Willoughby and Cade (1967) kept *P. namaqua* "up to a month without water in the absence of heat stress, being fed on dry bird seed only", and noted a "slow steady

weight loss" during dehydration. By losing weight somewhat more slowly during dehydration, and by seeming content to drink proportionately less when given water afterwards, *P. namaqua* showed evidence of being somewhat better adapted to water deprivation than *P. bicinctus*. This is consistent with the geographical ranges of the two species: despite a wide overlap in their occurrence, *P. namaqua* extends further into drier regions while *P. bicinctus* extends further into moister regions (Snow, 1978).

Responses to dehydration involved direct saving of body water by abolition of gular fluttering (i.e. evaporative water loss) together with other mechanisms (reduced ambulatory activity, longer periods spent sitting in the shade, increased feather erection, and, in *P. bicinctus*, reduced feeding) which would have reduced the metabolic and environmental heat load, and hence reduced the demands on body water reserves. McFarland and co-workers have described and discussed similar behavioural responses to dehydration in the Barbary Dove (*Streptopelia "risoria"*, probably a domesticated strain of *S. roseogrisea*: Parkes, 1971) (McFarland and Baher, 1968; McFarland and Budgell, 1970; McFarland and Wright, 1969).

The existence of well-developed responses allowing tolerance of water deprivation for a number of days makes it questionable whether individual sand-grouse drink daily. There is no direct evidence of drinking frequency by wild sand-grouse, but there is quantitative indirect evidence that they do indeed forego daily drinking. Willoughby and Cade (1967) (who also queried whether sand-grouse needed water daily) recorded crop water contents of *P. namaqua* shot at after drinking at one of the Namib Desert water-holes (Hotsas) as 16.4, 16.1 and 13.7% of body weight. If this represented replacement of weight loss of 3.4 g/100 g BW day due to dehydration (section 3.2), it would indicate a self-imposed water deprivation of 4.8, 4.7 and 4.0 days respectively in wild birds. A similar calculation indicates that wild *P. namaqua* observed drinking the normal 8–10 ships may have been without water for 3.3 to 4.1 days respectively. Thomas and Robin (1977) found fewer *P. alchata* and *P. orientalis* drinking on misty overcast mornings than on clear ones, and suggested that many individuals did not fly to water on days which were relatively cool. The advantages of not drinking daily would include energy saved for the round trip between feeding areas and drinking points, and avoidance of the predators (especially *Falco spp.*) which exploit sand-grouse flocks at water.

A corollary of the conclusion that sand-grouse may normally go several days between drinks is that the flocks attending a watering point on any day represent a correspondingly smaller fraction (perhaps 0.2 to 0.3) of the regional population and not the majority of birds as has usually been assumed. Total populations and population densities of sand-grouse may be several-fold higher, therefore, than the impression created by watching the sometimes enormous drinking flocks, and the success of

sand-grouse at exploiting a difficult unproductive habitat becomes all the more remarkable.

4.3 Foraging behaviour

There were pronouncedly different foraging techniques between *P. namaqua* and *P. bicinctus*, which are perhaps effective alternatives reducing competition and so promoting coexistence between species. The technique of searching a limited area thoroughly (*P. bicinctus*) seems to trade off the disadvantage of risking a smaller total available food stock within the foraging path for the advantage of relatively low energy costs harvesting the food requirement. On the other hand, making a cursory search of a large area (*P. namaqua*) seems to increase the chance of finding a sparsely distributed food supply, but at the expense of a higher energy cost obtaining it. A comparable pair of foraging techniques appears to occur in two coexisting species of North American desert rodents: *Perognathus* adopts a cursory extensive foraging pattern, while *Dipodomys* uses a locally intensive one, which results in the two species exploiting large and small seeds respectively, because of the differential effects of wind assortment on seeds of different sizes (Reichmann, 1979).

4.4 Social behaviour

Intraspecific competition for scarce food resources might be expected to lead to aggressive interactions or a hierarchical social structure amongst sand-grouse. However, food particles are generally very cryptic (see Dixon and Louw's (1978) Plate I), so that the first bird to see an item will eat it promptly (in all probability), making the item not worth a contest either on that account or on account of its relatively small size. Moreover, fighting (either actual or ritualised) in a hot open habitat has the multiple disadvantages of increased metabolic heat production, increased conspicuousness as a result of movement, and the danger of injury by a conspecific or predator. Thus, mutual yielding and a continued search for the means of existence may be a better investment of time and energy than aggressive or formalised competition between individuals.

It is not surprising, then, to find that social interactions within and between species could be summarised as pacific, undemonstrative, egalitarian gregariousness. The *P. namaqua* were caught as a single flock and so might conceivably have been a pre-existing social unit, but the *P. bicinctus* were caught piecemeal and so were probably not. If these species had a hierarchical social structure one might expect to see this directly in an established group, or else expect to see aggressive interactions until a hierarchy was established within a newly formed group. Since neither aggression nor hierarchy was observed, a pacific egalitarian social structure can be concluded to exist within non-breeding mixed-sex

groups of *P. namaqua* and *P. bicinctus*. In the absence of aggression, many intention movements, and threat and appeasement displays become irrelevant.

5 SUMMARY

Observations were made on captive Namaqua sand-grouse (*Pterocles namaqua*) and double-banded sand-grouse (*P. bicinctus*) at the Namib Desert Research Station and on wild birds.

Both species had well-developed behaviour patterns tending to reduce and disperse environmental and metabolic heat loads during the heat of the day and reduce heat loss by night. When air temperatures and solar irradiance were high, birds became relatively inactive, sought shade, insulated themselves by ptiloerection and forming huddles with other individuals, and sometimes dispersed heat by forced evaporative water loss (gular fluttering) and forced convection (wing drooping). Some of these responses were observed in wild birds also. At night, birds formed close huddles, which would have conserved metabolic heat by mutual insulation and ptiloerection, and by reduction of the radiant surface exposed to the sky (the major heat sink). Nocturnal huddling is also likely to reduce vulnerability to predators by promoting effective group vigilance.

Birds easily tolerated 3 days of water deprivation while exposed to the normal environmental heat load, losing weight by 3.4 – 4.4 g/100 g weight daily. This weight loss was made up partially (*P. namaqua*) or wholly (*P. bicinctus*) in one drinking session. Evidence is presented to suggest that wild *P. namaqua* may drink normally only every 3–5 days. Behavioural responses to dehydration can be interpreted as reducing water expenditure directly (abolition of gular fluttering) and indirectly (by further reduction of environmental and metabolic heat loads).

Interspecific differences in foraging behaviour suggest that this may promote ecological isolation between the species. Social behaviour was pacific and lacked hierarchical relationships between individuals. There was a corresponding lack of agonistic and signalling behaviour.

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