DESERT COLORATION IN BIRDS OF THE CENTRAL NAMIB DESERT

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(With 7 figures and 1 table)

INTRODUCTION

It is a well-known rule that ground-nesting birds tend to have plumage with colours and markings that conceal them from view when seen against the ground on which they live. This is especially so in deserts where ground cover is scarce, for there plumage frequently matches to a remarkable degree the colour tones and patterns of the ground on which the birds live. I shall use the term *desert coloration* to refer to this correspondence of plumage colour to ground colour in desert birds, but I shall not restrict its meaning to the "pale sandy isabelline" of Meinertzhagen (1954, p. 9). I shall describe the phenomenon of desert coloration as it occurs in the birds of the central Namib Desert, and discuss hypotheses about its function in light of the findings of this study.

Desert coloration in birds has long been noted, and in no other group of birds is it better developed than in the larks, family Alaudidae, which are typically small, ground-dwelling passerine birds of arid and semi-arid plains throughout Eurasia and Africa. Thus Kleinschmidt (1907, 1912) remarked on the plumage coloration in larks collected in Algeria, and (1912) published a colour plate showing the colour and pattern of soil samples taken from the collecting localities to show how the plumage of the local lark populations corresponded to the colour of their substrata. Subsequently other authors commented on desert coloration in birds, with special attention to larks in Arabia and northern Africa (Buxton, 1923; Cheesman, 1926; Bannerman, 1927). Hoesch and Niethammer (1940) published some excellent colour plates (1940, plates II, III, IV) depicting examples of most of the species of larks of South West Africa together with samples of the soils on which the specimens had been collected, with a chapter by Niethammer on the plumage colour of larks as a protective adaptation. Since then Hoesch (1959), Macdonald (1953b), Meinertzhagen (1951, 1954), Niethammer (1959), Vaurie (1951), and Watson (1962) have discussed aspects of desert coloration in larks and other birds. Heim de Balsac (1936), Kachkarov and Korovine (1942), Mayr (1942, 1963), and Hoesch (1956) have also discussed desert coloration in birds and other animals.

The observations on which this paper is based were made in the central Namib Desert, South West Africa in July and August, 1964, and from 17 July, 1965 to 10 July, 1966. The Namib Desert Research Station, Gobabeb (23°34′S, 15°03′E, 408 m) on the lower Kuiseb River about 60 miles southeast of Walvis Bay provided a base from which observations were made throughout the Namib Desert Park (formerly called Game Reserve Number 3).

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SOIL COLOURS OF THE NAMIB

The study area in the central Namib can be divided into two major geomorphic regions. The Great Sand Dunes extend southward from the Kuiseb River and the mouth of the Swakop River to the Orange River almost without interruption except in the vicinity of Lüderitz and Aus, and the Namib Platform extends northward from the Kuiseb and consists mainly of barren gravel flats (Logan, 1960). The colour of the dunes is a uniform pale rusty red, somewhat paler near the sea coast than near the eastern edge of the desert some 80 miles from the coast. The gravel flats are generally pale pinkish buff, varying from almost uniform very pale grey or white in some places to pale reddish brown with scattered white and pale pink quartz pebbles in others. Two colours named by Ridgway (1912) that approximate the general colour of the gravel flats are "salmon buff" and "light ochraceous salmon." Some limited areas in the gravel flats are dominated by black or dark grey stones, but these areas are exceptional, and there is nearly always an admixture of white or pinkish white pebbles and sand.

Thus the predominant colours of the Namib are pale rusty red, pinkish buff, pale grey and white, and the animals living there that have colouring dominated by these hues can be said to have desert coloration.

COLORATION OF THE BIRDS OF THE NAMIB

In order to describe the coloration of the birds of the Namib, one must first decide what species to call truly birds of the Namib Desert. In doing so I use the list compiled by Willoughby and Cade (1967, Table I, p. 13—18). Birds in that list which are excluded from consideration here as desertic species are those whose status in the central Namib is given as uncertain or rare, and those which occur primarily in Kuiseb Riverine Forest or Open Acacia Woodland habitats, as described in that paper. The birds that are here considered to be desert birds are those that conform to the following criteria: i) the nest is placed on the ground, or the birds spend much of their time foraging or resting on the ground, or both; ii) the species occurred in the study area through the entire year of observation (July, 1965 to July, 1966). All these species are listed in Table 1, with notes about colouring, nesting habits, the number of recognized subspecies in southern Africa, and whether the species occurs in the Namib as an endemic species or subspecies. The information on subspecies and endemism is included to indicate distributional tendencies in each species (for example, the designation of several subspecies usually indicates a wide geographic range with several localized breeding populations). In Table 1 the term *open nest* means that the nest and its contents are frequently open to view from above, while the term *concealed nest* means that the contents of the nest can not be seen from above because the cup is roofed over, or concealed by overhanging material such as vegetation, stones or earth.

Of the 21 species that fit the criteria for desert-birds of the Namib, seven have desert coloration, 12 have generalized dull grey or brown cryptic coloration, and five have conspicuous black and white markings. Thus some species are listed as having both cryptic coloration and conspicuous markings, because these species either have contrasting markings that can be concealed from view, or because one of the sexes is conspicuously coloured.

Birds with desert coloration

Heterotetrax rüppellii. — The small Rüppell's Bustard, or Rüppell's Korhaan, is endemic to the Namib and lives on the barren gravel flats. The dorsal plumage has a combination of pale delicate brown, pink and grey tints that give an overall pinkish buff colour which matches closely the soil colours of the Namib Platform. Hoesch and Niethammer (1940, p. 119) remarked on how well adapted this bird's plumage is to the colour of the Namib gravels. The long thin neck is light grey, and there are black markings at the sides and back of the head and a black stripe along the throat to the breast. These black markings are more pronounced in males, but are not very conspicuous, and in the field can be made out only at relatively close range.

Rüppell's Bustard lays its eggs on bare ground. One nest that I found in February, 1966, contained one egg and was on a completely bare patch of gravel. I did not see the incubating bird until it got up from the egg as I nearly drove over it with a Land Rover. At another time, a bird that I had

TABLE: **Coloration, type of nest, number of subspecies and endemism of birds of the Namib.**

Species	Desert coloration	Generalized Cryptic coloration	Conspicuous coloring	Open nest	Concealed nest	Species or subspecies endemic to Namib	Number of subspecies in southern Africa [1]
				(uses old nests of other birds such as crows)			
Greater Kestrel *Falco rupicoloides*		*		[1, 2]			1
Ludwig's Bustard *Neotis ludwigii*		*	*	* [1]			0
Rüppell's Bustard *Heterotetrax rüppellii*	*			* [1, 3]		*	2
Crowned Plover *Stephanibyx coronatus*		*	*	* [1]			1
Burchell's Courser *Cursorius rufus*		*		* [1]			0
Two-banded Courser *Hemerodromus africanus*	*			* [1]			3
Namaqua Sandgrouse *Pterocles namaqua*		*		* [1, 3]			0
Large-billed Sabota Lark *Mirafra naevia*		*			* [1]	* [2]	4
Karroo Lark *Certhilauda albescens*	*				* [1]	*	7
Spike-heeled Lark *Certhilauda albofasciata*	*			* [1, 3]		*	16
Stark's Lark *Spizocorys starki*		*		* [1, 3]			0
Grey-backed Finch-lark *Eremopterix verticalis*		*	*	* [1, 3]			3
Gray's Lark *Ammomanes grayi*	*			* [3]		*	2
Chat Flycatcher *Bradornis infuscatus*		*		* [1]			4
Mountain Chat *Oenanthe monticola*			*		* [1]		4
Layard's Chat *Oenanthe tractrac*	*		*		* [1, 3]	*	4
Familiar Chat *Cercomela familiaris*		*			* [1, 3]		8
Schlegel's Chat *Emarginata schlegelii*	*		*		* [1, 3]	*	4
Southern Anteater Chat *Myrmecocichla formicivora*			*		* [1, 3]		2
Scaly-fronted Weaver *Sporopipes squamifrons*		*			* [1, 3]		0
Lark-like Bunting *Fringillaria impetuani*		*		* [1, 3]			2

[1] Mackworth-Praed and Grant (1962, 1963) [2] Hoesch and Niethammer (1940) [3] This study

wounded crouched on the gravel and I could not see it for several minutes until it flew up a few feet from me as I searched for it.

Hemerodromus africanus. — The Two-banded Courser in the Namib has generally pale sandy buff dorsal colour that results from the light brown centers and broad, pale buff edges of the dorsal feathers. The legs and feet are white. The paleness of the colouring of this species in the Namib makes it difficult to make out against the glaring gravel flats where it lives.

Certhilauda albescens. — The Karroo Lark has been divided into eight or nine subspecies that differ mainly in plumage colour and pattern (Macdonald, 1953a; Lawson, 1961), depending on the colour and pattern of the ground where they live. The Red-backed Karroo Lark *C. a. erythrochlamys* that occurs in the central Namib is one of the more striking examples of a subspecies matching its background. It lives in the dunes from the Kuiseb River to the vicinity of Aus and Lüderitz Bay, wherever scattered clumps of tall spiny grasses occur; and its unmarked pale rusty-red dorsal plumage matches nearly perfectly the smooth rusty-red sand on which it lives (Figure 1). Other subspecies which live on stony or pebbly soils have more or less pronounced spotting or streaking.

Certhilauda albofasciata. — The Spike-heeled Lark is also a polytypic species that has been divided into as many as 16 subspecies which differ mainly in plumage colour and pattern (Meinertzhagen, 1951; Macdonald, 1953b; Winterbottom, 1958), and tend to match the colour of the ground of their respective ranges (Hoesch and Niethammer, 1940; Macdonald, 1953b). The spike-heeled larks in the Namib Desert Park live on the gravel flats at the eastern edge of the desert where scattered low scrubs occur. They are among the palest of the species. Figure 2 shows a freshly-killed adult lying where it fell about three miles east of the Gross Tinkas water-hole. It is probably referable to the subspecies *C. a. boweni* which is one of the palest of the described subspecies. Figure 3 shows a young fledgeling, still unable to fly, in a characteristic pose taken about 11 miles southeast of where the adult was photographed.

Ammomanes grayi. — Gray's Lark is endemic to the Namib where it inhabits the barren gravel flats. Its dorsal plumage matches the colour of the gravel surface very closely, and a bird squatting motionless on the open ground or on a nest is virtually invisible to the human eye from only a few feet away. Incidentally, when a bird stands upright on the gravel with its white breast in view, it has a remarkable resemblance to the ubiquitous pinkish white quartz pebbles of its habitat; so this species is always hard to see in the field unless it moves. Figure 4 shows two adult birds on the ground where they were collected, and Figure 5 depicts a young fledgeling several days before it is able to fly, showing the remarkable concealing effect of the plumage colouring.

Oenanthe tractrac. — The Layard's Chat is a pale desert wheatear that has been divided into four subspecies ranging from the western Cape Province to Angola (Mackworth-Praed and Grant, 1963, p. 145—146). The subspecies occurring in the central Namib, *O. t. albicans,* is the palest of them, being a very pale grey dorsally and white ventrally, with white upper tail coverts and base of tail and blackish brown on the rest of the tail. The tail shows conspicuously only when the bird is flying. Figure 6 depicts a freshly killed bird where it fell near Swartbank Mountain. It is a bird of the barren gravel flats.

Emarginata schlegelii. — Schlegel's Chat is very similar in colour to Layard's Chat, but in the study area it has a slightly darker shade of grey on the back and a blacker tail. Instead of living on barren gravel flats, it stays in areas with scattered bushes along the eastern edge of the desert; and it is actually a bird of arid or semi-arid scrub rather than barren desert. Desert coloration in this species is not as strongly developed as in the birds listed above, and I include it in this category not because it is a very good example of desert coloration, but primarily because it is similar in colour to *Oenanthe tractrac albicans,* and because the palest subspecies, *E. s. schlegelii,* occurs in this part of the Namib.

Birds with generalized cryptic coloration

The birds with plumage coloured dull brown or grey or streaked and mottled with combinations of brown and grey are considered to have generalized cryptic coloration because their colours tend to conceal them from view on a variety of substrata. In many instances this colouring serves remarkably well to conceal these birds on Namib soils, but because their plumage colours are not dominated by the typical hues of Namib soil, I do not consider them to have desert coloration. Here I list these species from Table I and give some brief notes on their biology in the central Namib.

Falco rupicoloides. — The Greater Kestrel occurs everywhere on the gravel flats of the central Namib, and is widespread in arid and semi-arid regions of Africa. It spends much time perched on the ground or on rocks in the gravel flats, where its tawny mottling makes it hard to see from a distance.

Neotis ludwigii. — Ludwig's Bustard occurs sparingly all over the gravel flats, but is most abundant in the eastern half of the desert where some grass and scrub occur. The brown mottling of its dorsal plumage is a considerably darker shade than the soil of the Namib. It is widespread outside the Namib.

Stephanibyx coronatus. — The Crowned Plover occurs sparingly on gravel flats along the eastern edge of the Namib Desert Park. Its uniformly medium-brown dorsal plumage is a darker shade than most Namib soils. It is widely distributed in Africa.

Cursorius rufus. — Burchell's Courser occurs on gravel flats in the eastern half of the Namib. Its light-brown unmarked dorsal plumage is a somewhat darker shade than most Namib soils. It is distributed throughout arid and semi-arid southern Africa, and is subject to local movements (McLachlan and Liversidge, 1957).

Pterocles namaqua. — The Namaqua Sandgrouse is another species that occurs throughout arid and semi-arid southern Africa. In the Namib it lives on the gravel flats, and its distribution is influenced by the location of watering places such as the Gross Tinkas water-hole and the game watering installation at Hotsas (Willoughby and Cade, 1967). It tends to move locally according to rains (Mackworth-Praed and Grant, 1962). Its mottled light-brown and buff dorsal plumage is a somewhat darker shade than most Namib soils.

Mirafra naevia. — The Large-billed Sabota Lark (considered conspecific with *M. sabota* by some authors) is a bird of the semi-arid bush-steppe of the highlands east of the Namib, and occurs in the Namib only near its eastern edge where suitable habitat with scattered bushes appears. Its light brown streaked plumage is effective in concealing it on a variety of pale soils, but it lacks a predominance of hues of the Namib soils. However, it is a polytypic species that tends strongly to match the colour of the soils on which it lives (see Hoesch and Niethammer, 1940, Plate II).

Spizocorys starki. — Stark's Lark lives on the gravel flats wherever there are extensive areas with sparse grass resulting from local rainfall. This species moves about in flocks, and settles to breed in the Namib where green grass is produced by summer and autumn rainfall. It is widespread in southern Africa and its tendency to wander in search of suitable breeding conditions brings it into contact with arid and semi-arid soils of diverse coloration. While it is generally a pale streaked brown above (Figure 7), there is a good deal of individual variation in colouring so that birds in the same flock may be paler or darker, greyer or browner or more reddish, and they seldom have the same colouring as the soil. This individual colour variation was noted by Hoesch and Niethammer (1940, p. 227).

Eremopterix verticalis. — The Grey-backed Finch-lark is just like the Stark's Lark in its occurrence in the Namib, differing only in that it more readily forages on sandy ground such as dry stream beds and washes, and sometimes appears in the sand dunes. Besides showing the same kind of individual colour variation as the Stark's Lark, the Grey-backed Finch-lark also has marked sexual colour dimorphism. Immature birds and adult females are streaked brown and grey, very similar in appearance to the Stark's Lark except for a black patch on the abdomen that is invisible except when seen from beneath. Mature males, however, are conspicuously marked with black and white patches on the head, and a black breast. This makes the males very conspicuous against the pale soils of the Namib. The species occurs widely in arid to semi-arid parts of southern Africa, and it also wanders in search of suitable breeding habitat.

Bradornis infuscatus. — The Chat Flycatcher occurs in the gravel flats in bushy areas near the eastern edge of the Namib. It is a uniform pale brown dorsally, of somewhat darker shade than most Namib soils. It is widely distributed in southern Africa.

Cercomela familiaris. — The Familiar Chat occurs in the Namib gravel flats wherever there are boulder-strewn rock outcrops and *koppies*. It is a uniform light brown above, with a rufous tail. It is found throughout southern Africa.

Sporopipes squamifrons. — The Scaly-fronted Weaver occurs in the Namib where scattered bushes occur adjacent to grassy gravel flats such as along the dry stream courses running westward into the Namib Platform from the eastern highlands. Little flocks nest in thorn bushes and feed on the ground among the sparse grasses. This tiny bird is light grey above, with black flight feathers edged with white, black malar stripe and black feathers on the forehead. Juveniles are browner and lack the black feathers on the head. It occurs widely in arid and semi-arid southern Africa.

Fringillaria impetuani. — The Lark-like Bunting is a pale streaked brown bird that flocked onto the gravel flats to breed where late summer and autumn rainfall induced the growth of annual grasses. Its pale streaked brown plumage conceals it on a variety of pale brown soils. It lives in drier areas throughout southern Africa, and has a notable tendency to wander (Skead, 1960, p. 124). A colour figure of this species occurs in Skead (1960, Plate XIX opposite p. 122).

Birds with conspicuous markings

These birds fall into two groups, cryptically coloured birds with conspicuous markings that can be concealed from sight, and birds with the whole plumage conspicuously marked.

Neotis ludwigii. — The wings have contrasting black and white flight feathers that can be seen at a great distance when the bird flies.

Stephanibyx coronatus. — There are contrasting black and white markings on belly, wings and tail,

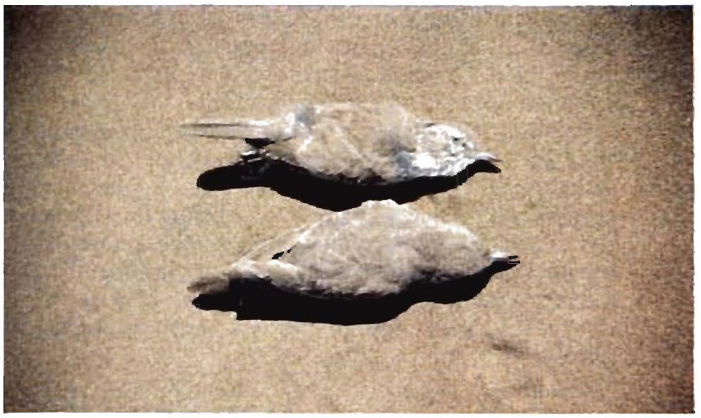

Figure 1:

Red-backed Karroo Larks on dune sand where they were collected, 10 miles south-east of the Namib Desert Research Station, 21 April, 1966. These birds were molting, and the new feathers which had not yet faded were slightly darker red than the sand.

Figure 2:

Adult Spike-heeled Lark lying where it was shot about 3 miles east of Gross Tinkas, Namib Desert Park, 4 October, 1965.

Figure 3:

A young fledgeling Spike-heeled Lark resting in the shade of a tuft of grass at the western border of Farm Onanis, 6 May, 1966.

Figure 4:

Two adult Gray's Larks on the ground where they were collected, 5 miles south-east of Hotsas, Namib Desert Park, 8 May, 1966.

Figure 5:

A young Gray's Lark just out of the nest, 10 miles northeast of Zebra Pan, Namib Desert Park, 25 May, 1966.

Figure 6:

Adult Layard's Chat where it was shot near Swartbank Mountain, Namib Desert Park, 5 June, 1966.

Figure 7:

Stark's Lark, adult and two young. The adult is in the act of feeding one young bird that has just tottered from the nest and is obscured by the adult, while the other nestling stands in the nest and begs. The back of the adult lacks the pinkish buff tints of the soil which the Spike-heeled Lark and Gray's Lark have. Eight miles northeast of Zebra Pan, Namib Desert Park, 25 May, 1966.

nspicuous when the bird flies. There are less nspicuous black and white markings on the crown.

Eremopterix verticalis. — The mature male has nspicuous black and white plumage.

Oenanthe tractrac. — The black and white tail is nspicuous in flight.

Emarginata schlegelii. — The same as *Oenanthe ctrac.*

Oenanthe monticola. — Both sexes of the Mountain at are contrastingly marked with black and white, t the male has the most striking pattern, which rather variable from one male to another. It urs in the Namib wherever there is rough rocky terrain such as in canyons and around *koppies*. It is widely distributed in southern Africa.

Myrmecocichla formicivora. — The Southern Ant-eater Chat occurs on gravel flats along the eastern edge of the desert, where it nests in the burrows of the Aardvark *Orycteropus afer*. In the field it appears black, with a white patch near the tip on the wing which flashes as the bird flies. The male also has a large white patch on the upper side of the wing between wrist and body. This species is conspicuous on the pale Namib gravel, especially when flying. It occurs over much of semi-arid southern Africa.

DISCUSSION

Common characteristics of birds with and without desert coloration

It would be helpful now to examine the data on coloration and biology of birds of the Namib compiled in Table I to see whether there are any patterns that may give clues about the function of desert coloration.

In the seven species that have desert coloration, four have open nests and three have nests that are usually concealed. The latter are the Karroo Lark, which builds a domed nest under bushes (Maclean, 1957; Mackworth-Praed and Grant, 1962); Layard's Chat, which nests under stones or bushes (Mackworth-Praed and Grant, 1963; this study), or even inside the mouths of rodent burrows (this study); and Schlegel's Chat, which nests under stones, bushes or tufts of grass (Mackworth-Praed and Grant, 1963). Two species are endemic in the Namib and four are represented by subspecies endemic in the Namib. Of the five species with desert coloration that have wide distribution outside the Namib, none has less than three described subspecies, while the Karroo Lark has up to nine (Lawson, 1961), and the Spike-heeled Lark has 16 (Winterbottom, 1958). A large number of subspecies indicates that the species tends to be sedentary without much genetic mixing between local populations.

Of the 12 species that have generalized cryptic coloration, seven have open nests, four have nests that are usually concealed somehow, and one, the Greater Kestrel, frequently uses the abandoned nests of other large birds such as crows. Only one of these species has a subspecies that is more or less restricted to the Namib, namely *Mirafra naevi uis* (= *M. sabota uis*), described by Hoesch and Niethammer (1940, p. 218) as inhabiting the Inner Namib *("Vor-Namib")* north of the Swakop River. Sabota larks occurring in the Namib Desert Park are probably referable to this subspecies. Seven of these species have either no subspecies or only 1 subspecies in all of southern Africa, one has 2 subspecies, one has 3, two have 4 and one has 8 subspecies. A small number of subspecies indicates a tendency for rapid genetic mixing throughout the population, which may result when individuals tend to wander from one region to another within the range of the species.

The two species that have conspicuous black and white coloration all the time, the Mountain Chat and the Southern Ant-eater Chat, nest in protected places among stones (Mountain Chat) or under ground (Ant-eater Chat).

The foregoing observations indicate that all of the birds with desert coloration are more or less sedentary, with a tendency for local populations to assume the colours of the ground on which they live. Of the birds that have generalized cryptic coloration, the majority ($^3/_4$) have three or fewer described subspecies, indicating a tendency for individuals of these species to wander within the species range. There is no clear tendency to have the nest open or concealed in either group.

The function of desert coloration

The question of the function of desert coloration has puzzled some investigators. Since desert coloration serves admirably to conceal the motionless animal from view when it is seen against its natural background by the human eye, it is quite reasonable to assume that desert coloration conceals the animal from the view of its natural predators such as hawks and falcons. Although the simplest explanation of desert coloration is that it is protective against predation (Vaurie, 1951, p. 446), several authors have been reluctant to accept this explanation. Buxton (1923, p. 168 — 169) felt compelled to abandon the theory of protective coloration because it seemed difficult to apply it to those desert animals that are active at night, or to animals that do not seem to have any large enemies more powerful than themselves, or because regardless of how well their colour blends with the surroundings the concealing effect is lost when they move. Meinertzhagen (1954, p. 8—31), while he considered desert coloration to be very good camouflage in many instances, could not accept this explanation for the desert coloration in nocturnal and fossorial animals, or in birds such as swifts and martins that feed on the wing, and he expressed his perplexity at what seemed to be contradictory evidence for the protective function of desert coloration. Hoesch (1959) thought that cryptic coloration in birds of the Namib had no protective function against predators because, he said, these birds had no important predators in the Namib. Heim de Balsac (1936) and Kachkarov and Korovine (1942) expressed similar doubts about the function of desert coloration as protection against predation. These authors thus could only suggest that desert coloration originates from some direct action on the individual of environmental factors such as humidity or soil colours, or from some active process arising within the individual.

Despite their objections to the theory that desert coloration is protective against predation, it is certainly much easier to accept this theory rather than their hypotheses of mysterious direct environmental action or endogenous physiological processes. Although Hoesch (1959) believed that here were no important predators of birds in the Namib, it is a fact that there are several species of hawks and falcons and two species of crows (Willoughby and Cade, 1967) that are potential predators on small birds there. In fact, on several occasion in the Namib I saw lanners, *Falco biarmicus,* trying to catch Grey-backed Finch-larks by swooping low over flocks on

the ground and striking at individuals that took flight; and I watched a lanner kill a Namaqua Sandgrouse using the same hunting tactics. Besides diurnal avian predators, there are several mammalian carnivores in the Namib that according to my observations are active during daylight, quite conceivably prey on birds (particularly flightless young) and may locate prey by sight. These are Bat-eared Fox *Otocyon megalotis,* Black-backed Jackal *Canis mesomelas,* Yellow Mongoose *Cynictis penicillata* and Suricate *Suricata suricatta.*

It is worth mentioning here the elementary concept in the theory of natural selection that a genetic characteristic, such as light or dark pigmentation, needs to be of advantage to individuals only during part of the life-cycle say as protection for incubating adult birds or fledgelings — in order for it to be established and preserved in the population, so long as this characteristic does not present too great a disadvantage to the species at other times. Also, a very small selective advantage is all that may be needed to establish such a characterstic in a population.

The idea that desert coloration can not be protective against predation by owls at night is contradicted by the experiments of Dice (1947) on the effectiveness of predation by owls on deer mice, *Peromyscus maniculatus,* in captivity. In these experiments live deer mice of different colours were exposed together to predation by a barn owl, *Tyto alba,* in very dim light on floors covered with different coloured soils, and in such a way that the owl could not capture prey by sound alone. The results clearly showed that the owl captured significantly fewer of the mice that were coloured like the soil (*e.g.* buff mice on buffy soil) than those that contrasted with the soil (*e.g.* grey mice on buffy soil). This difference in susceptibility to predation by the owl was consistent even at light intensities estimated by Dice to be as low as 8×10^{-8} = 0.00000008 foot-candles.

Pale desert coloration may offer advantage other than concealment from predators. It has been suggested that desert coloration may serve to protect animals against heat and light (Heim de Balsac, 1936, p. 341; Vaurie, 1951, p. 445—446). Indeed, pale plumage absorbs less energy in the visible spectrum than dark plumage, and the lowered absorption of heat by plumage in the hot sun might result in a reduced expenditure of water evaporated to keep the bird's body temperature at a tolerable level. An experiment by Hamilton and Heppner (1967) using white domesticated zebra finches, *Taeniopygia castanotis,* which were coloured black with vegetable dye showed that at an environmental temperature of 10°C. the black-dyed birds consumed 23 percent less oxygen per gram of body weight than white birds when both were exposed to a bright sun lamp. This indicated that the blackened plumage absorbed more radiant energy from the lamp than the white plumage, thus reducing the net rate of heat loss from the blackened birds. It then appears reasonable to suppose that desert birds with pale coloration do benefit somewhat from the reduced energy absorption in hot sunshine in keeping the body temperature within tolerable limits, for they would conserve water that they otherwise would evaporate to dissipate the heat. Nevertheless, I believe that the primary function of pale plumage in a pale desert is concealment. The desert lark *Ammomanes deserti* of Arabia and north Africa matches the colour of the ground on which it lives, be it black lava desert or very pale desert (Cheesman, 1926, p. 318; Meinertzhagen, 1954, p. 17); so concealment from view on the black desert soil must be more important to the survival of individuals of this species than is the reflection of visible light and the consequent reduction of heat transfer to the bird's body. I see no reason to believe this is not so with other concealingly coloured birds.

One last question that ought to be considered is how to account for black desert-birds that clearly are not concealingly coloured. The Southern Ant-eater Chat and the Mountain Chat are examples in the Namib, and there are other examples of black or black and white chats in the Palaearctic deserts (Buxton, 1923, p. 154—155; Heim de Balsac, 1936). It is interesting to note that the males of the two black and white chats of the Namib are more conspicuously marked than the females, which suggests that these conspicuous markings function in a social context — perhaps for species recognition or sex recognition, or both — and one can only assume that conspicuous coloration is at least as valuable for their survival as is cryptic coloration. These two species nest in hidden places, so that they are relatively safe from predators that hunt by sight when they are in the nest, unlike many of the concealingly coloured species. They also spend much of their time foraging near burrows (Ant-eater Chat) or rocks and boulders (Mountain Chat) where they can quickly duck under cover if attacked. Staying close to cover such as this may be the price these species have to pay for having conspicuous coloration.

Finally, then, it appears reasonable to say that desert coloration in birds is generally an adaptation for concealing them from predators such as falcons and hawks in an environment that provides little protective cover, and that it reaches its highest development in sedentary localized populations which have had a long time for natural selection to act on plumage colour with little genetic influence from other populations of the species. In those species with more generalized cryptic colouring, the individuals tend to wander within the species range onto a variety of differently coloured soils, so natural selection has resulted in colour patterns that

tend to conceal them on a number of desertic and semi-desertic soils. A few species have assumed conspicuous plumages, possibly connected with intra-specific and interspecific social interactions.

SUMMARY

Many desert birds have plumage coloration that matches the colour of the ground on which they live. They have what is called desert coloration. Birds that have desert coloration in the Namib Desert Park, central Namib Desert, South West Africa are Rüppell's Bustard, Two-banded Courser, Karroo Lark, Spike-heeled Lark, Gray's Lark, Layard's Chat, and Schlegel's Chat. Other birds have a generalized cryptic coloration of dull or streaked browns and greys, and in the central Namib these are Greater Kestrel, Ludwig's Bustard, Crowned Plover, Burchell's Courser, Namaqua Sandgrouse, Large-billed Sabota Lark, Stark's Lark, Grey-backed Finch-lark, Familiar Chat, Chat Flycatcher, Scaly-fronted Weaver and Lark-like Bunting.

The birds with desert coloration tend to be sedentary and to occur in the Namib as endemic species or subspecies, while those with generalized cryptic coloration tend to be widely distributed outside the Namib without forms endemic to the Namib and with few subspecies. A few species are conspicuously coloured.

The theory that desert coloration is protective against predation has not been accepted by every student of the subject; but observations on the birds of the Namib revealed no reason to reject this theory. Although pale desert coloration may be useful to a bird in conserving water when exposed to hot sunshine owing to reduced absorption of heat in the visible spectrum by the plumage, this probably is not a significant factor in determining the coloration of desert birds in general.

Those few desert birds that are conspicuously black and white may be so coloured for intra- and inter-specific social reasons that are more important for the survival of the species than is camouflage.

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