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## EVOLUTIONARY TRENDS IN THE SANDGROUSE (PTEROCLIDAE)

by G.L. Maclean

Received 14 April 1984

The main concentrations of sandgrouse species today are from North Africa (mainly the southwestern Sahara) through the Middle East to the Thar Desert of northwestern India (Maclean 1976). It seems likely therefore that the family has its centre of radiation somewhere within this major arid region of the world, and it is here that the most likely ancestral type of sandgrouse is to be found. Within the 16 species of sandgrouse, two fairly clearly defined genera can be identified mainly on the basis of foot structure: *Syrnhaptēs* has the front toes completely enclosed in a podotheca and the entire tarsometatarsus and toes are feathered; *Pterocles* has the front toes separate and naked, and the tarsometatarsus feathered anteriorly only. The hind toe is absent in *Syrnhaptēs*, vestigial in *Pterocles*. However, basic plumage similarities between these genera are easily recognizable, and plumage criteria can be used to identify all the major evolutionary trends among sandgrouse.

A basic plumage pattern can be traced in the two species of *Syrnhaptēs* (both Palaearctic in distribution) and in most of the Palaearctic species of *Pterocles* (Fig. 1). The one extant species of sandgrouse that comes closest to a composite picture of the basic pattern is *P. orientalis* which differs from the hypothetical ancestral plumage pattern only in lacking elongate central rectrices. This hypothetical ancestral type can therefore be termed the ancestral "orientalis-type" sandgrouse; from it arose at least five major evolutionary lines by relatively simple processes of retention, reduction, loss or development of certain plumage characteristics, as well as some modifications of other structures (especially the legs and feet) and of behaviour. It may be assumed that the ancestor arose in North Africa or the Middle East.

The first of these evolutionary lines involves the loss of the long central rectrices and leads to *P. orientalis* itself. The second leads to the somewhat aberrant *P. alchata* by a series of relatively small changes. The third (and possibly the oldest) involves modifications not only of plumage, but also of foot structure (no doubt as an adaptation to low environmental temperatures in arid Central Asia), and gave rise to the two species of *Syrnhaptēs*; even here, plumage changes are relatively minor. A fourth line migrated southeastwards, giving rise to *Pterocles exustus* in East Africa and *P. namaqua* in southern Africa; the complete allopatry of their present distribution is consistent with the requirements for speciation in different habitats, and both species retain many ancestral plumage features.

The fifth main evolutionary line derived from the ancestral "orientalis-type" sandgrouse has led in turn to another major evolutionary radiation, mainly involving the loss of the long central rectrices and the development of a black-and-white pattern on the forehead of the male. The least differentiated species on this line are *P. senegallus* and *P. coronatus*,

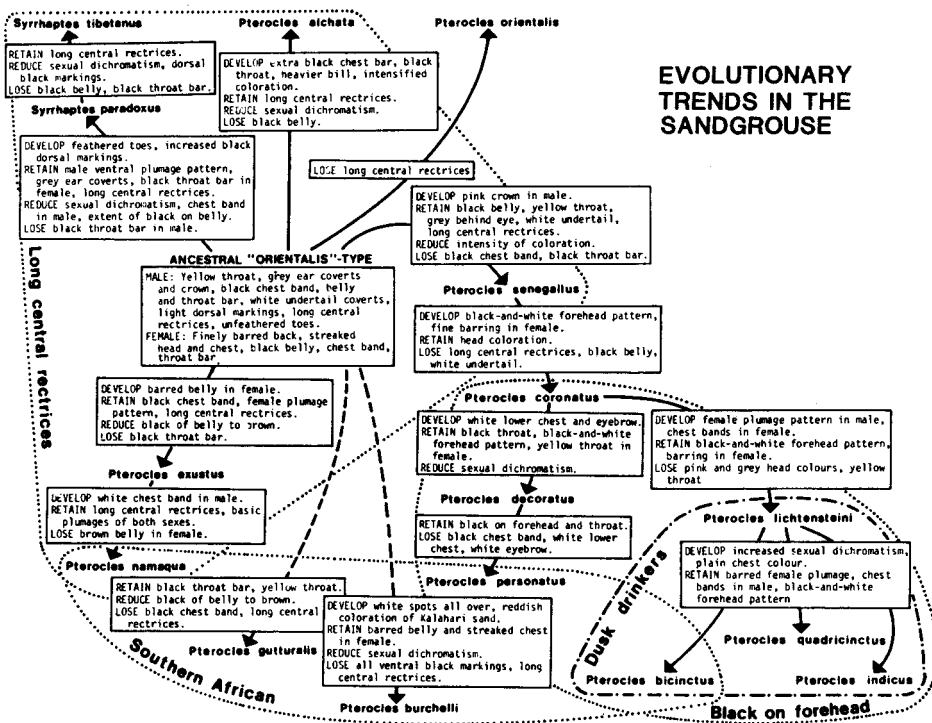


Table 1 Comparison of the groupings of sandgrouse by Maclean (this study) and by Wolters (1974)

Species	Group No. (Maclean)	Genus (Subgenus) (Wolters 1974)
<i>paradoxus</i>	2	<i>Syrhaptus</i> ( <i>Syrhaptus</i> )
<i>tibetanus</i>		-----
<i>orientalis</i>	3	<i>Syrhaptus</i> ( <i>Eremialector</i> )
<i>gutturalis</i>		-----
<i>alchata</i>	1	<i>Pterocles</i>
<i>exustus</i>		-----
<i>namaqua</i>	4	<i>Nyctiperdix</i> ( <i>Namapterocles</i> )
<i>senegallus</i>		-----
<i>coronatus</i>	5	<i>Nyctiperdix</i> ( <i>Parapterocles</i> )
<i>decoratus</i>		-----
<i>personatus</i>	7	<i>Nyctiperdix</i> ( <i>Macleanornis</i> )
<i>quadricinctus</i>		-----
<i>bicinctus</i>	5	<i>Nyctiperdix</i> ( <i>Nyctiperdix</i> )
<i>indicus</i>		-----
<i>lichtensteini</i>	7	<i>Nyctiperdix</i> ( <i>Dilophilus</i> )
<i>burchelli</i>		<i>Calopteroles</i>

still both inhabiting the ancestral Palaearctic arid zone, including North Africa. Apparently related, somewhat geographically removed, but with relatively little modified plumage pattern (except for the highly characteristic white lower chest and eyebrow) is *P. decoratus* of East Africa. The derivation of the endemic Madagascan *P. personatus* from *P. decoratus* is speculative, but *P. personatus* undoubtedly derives from the *senegallus-coronatus* line as evidenced by its black forehead.

From somewhere along this fifth line of evolution, probably from a species similar to *P. coronatus*, arose the well defined subgroup of four species *P. lichtensteini*, *P. quadricinctus*, *P. bicinctus* and *P. indicus*, sometimes classed as a separate genus *Nyctiperdix*. These become progressively more differentiated from the North African *lichtensteini*-type the further they are removed geographically, leading to *P. bicinctus* in southern Africa on the one hand, and to *P. indicus* in India on the other.

The southern African *P. gutturalis* is widely separated geographically from the ancestral home of the family, but it retains some of the ancestral plumage features, although aberrant in many ways. The most highly aberrant species of sandgrouse, relative to the "*orientalis*-type", is *P. burchelli* of southern Africa, with the most widely divergent plumage and structural characters; its general coloration is that of the red Kalahari sand where it lives, and it has proportionately much the longest legs of any sandgrouse. *P. gutturalis* and *P. burchelli* appear to represent two relatively old and independent invasions of southern Africa. *P. namaqua* surely represents a more recent invasion, with features far closer to the ancestral type.

According to the plan above, the sandgrouse fall into six or seven more or less well defined groups, each of which might qualify as a subgenus, although not all of equal rank.

Group 1 is characterized long central rectrices and a mainly Palaearctic distribution, the chief exception being *P. namaqua*. It includes the species *alchata*, *exustus*, *senegallus* and *namaqua*.

Group 2 is characterized by joined and feathered toes, no hind toe, and an Asian distribution; it is usually recognized as the genus *Syrrhaptes* with the two species *paradoxus* and *tibetanus*. In its plumage features it is not far removed from the hypothetical "*orientalis*-type".

Group 3 consists only of *orientalis*, separable from Group 1 only by the absence of elongate central rectrices.

Group 4 is characterized by black forehead coloration in males, and a loss of long central rectrices. It includes *coronatus*, *decoratus* and *personatus*, and leads naturally to the next group.

Group 5 is the best defined group of sandgrouse, forming the *Nyctiperdix* complex (possibly a superspecies) of *lichtenstein*, *quadricinctus*, *bicinctus* and *indicus*. It is characterized by heavily barred plumage patterns, black-and-white foreheads in the males, and nocturnal or crepuscular activity patterns (especially drinking behaviour).

Group 6 consists only of *gutturalis* which may be closer to *P. orientalis*

than its present plumage features and geographical distribution indicate. It has lost the elongate central rectrices of the ancestral form, but retains several "orientalis-type" features.

Group 7 consists only of *burchelli* whose characteristics have already been discussed above.

Comparing my groupings with those of Wolters (1974), several similarities emerge. One of the most obvious is the recognition of the subgenus *Nyctiperdix* (my Group 5) and its inclusion within a larger complex of species with black foreheads which Wolters raises to the rank of genus *Nyctiperdix* (my Group 4 in part). Some details of arrangement within these divisions differ, but their affinities are indicated. Wolters also recognizes the closeness of *Syrnhaptes* (*sensu stricto*) with the other long-tailed species of sandgrouse. Interestingly too, Wolters places *orientalis* and *gutturalis* together as the subgenus *Eremialector*, agreeing with my suspicions that they may indeed be closely related. Although *P. alchata* is rather aberrant, I do not believe it warrants separate generic status as proposed by Wolters. Finally Wolters and I also agree about the extreme specialization of *P. burchelli* which he places in the monotypic genus *Calopteroles*.

On the whole I do not believe it is necessary to divide the sandgrouse into more than two genera, *Pterocles* and *Syrnhaptes*, as they are usually defined. I do, however, agree that subgeneric division is valid, though my seven groups do not coincide exactly with the nine subgenera of Wolters (1974). A direct comparison of the two plans appears in Table 1.

#### REFERENCES

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