

Viewpoint

Possible mechanisms of substrate colour-matching in larks (Alaudidae) and their taxonomic implications

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The larks (Alaudidae) comprise a family of around 100 terrestrial and largely cursorial passerine species spread across a relatively large number of genera (Juana *et al.* 2004, Alström *et al.* 2013, del Hoyo & Collar 2016). Many larks, particularly widespread and sedentary species of deserts and other arid habitats, show a remarkable degree of intraspecific geographical variation in plumage colour tones. Many species have been divided into a large number of subspecies largely or wholly on the basis of this colour variation (de Juana *et al.* 2004). It has long been recognized, perhaps first by Kleinschmidt in the first years of the 20th century (Niethammer 1940), that this variation in plumage colour is closely correlated with the colour of the substrate (sands, soils or rocks) that the different populations inhabit (e.g. Bannerman 1927, Bates 1936, Niethammer 1940, Meinertzhagen 1951, Vaurie 1951, Macdonald 1953, Mayr & McEvey 1960, Archer & Godman 1961,

Dean & Williams 2004); dark larks occupy dark soils or rocks, red larks occupy red sands, and pale larks occupy pale substrates. We are not aware of any attempt to quantify this correlation empirically, but the pattern has been described in detail so many times that it appears worthy of investigation. Writing with specific reference to larks in the arid regions of Somaliland (Somalia), Archer and Godman (1961) wrote: 'The close relationship between the colour of the soil and the colour of the bird, whatever may be its origin, is undoubted; it permits of no argument or dispute. In all the cases of Larks cited above the relationship is exact and complete, and, practically speaking, *there is no exception to the rule*' (original authors' own emphasis). Mayr and McEvey (1960), in their study of the variation in colour of Horsfield's Bushlark *Mirafra javanica* in Australia, concluded: 'It is now evident that the coloration of larks does not respond, like that of other birds, primarily to general features of climate which would result in gradual clinal changes. Rather, each population is selected to blend with the prevailing colour of the local soil on which the birds spend most of their life.' The same authors pointed out that this has the result that adjacent subspecies that occupy different substrates can look very different from each other, whereas widely allopatric subspecies that occur on similarly coloured substrates can look practically identical. Of the most extreme example of substrate colour-matching, the Desert Lark *Ammomanes deserti*, Bates (1936) pointed out that 'A map of Arabia coloured to match exactly the freshly moulted back-plumage of the Larks of this group inhabiting each locality would be a patchwork of very different colours, not always gradually shading off into the surrounding ones, but changing abruptly; e.g., dark-slate birds are found very near sandy-isabelline ones.' The same author noted that colour variation in Desert Larks is intimately linked to the underlying geology, with dark forms occurring on dark igneous substrates and pale forms on sandy sedimentary substrates. Similarly, Crested Larks *Galerida cristata* occupying the rich alluvial soils of the Nile Valley and Delta are much darker than the pale forms of the adjacent sandy deserts just a few kilometres away (Cramp 1988, de Juana *et al.* 2004). Niethammer (1940) was so struck by the relationship that he followed Kleinschmidt's earlier example and collected soil samples when he collected lark specimens in south-western Africa, finding that the pattern was as obvious in the laboratory as it was in the field. There are many other examples. Species conforming to this pattern can be found in all six major sub-clades identified by a recent molecular phylogeny of the whole family (Alström *et al.* 2013). The same pattern of substrate colour-matching has been described in certain mammals (e.g. Harrison & Seton-Browne 1969, Vignieri *et al.* 2010). However, it is not apparent in all larks (e.g. it is absent in many nomadic or migratory species) nor is it

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described for more than a handful of species in other terrestrial groups of passerines that occupy similarly diverse substrate environments, such as the pipits (*Anthus*). If the pattern is not unique to the larks, then it certainly finds its strongest expression within the family.

Processes of substrate colour-matching

The extraordinarily close colour-matching between the plumage of certain larks and the substrates they occupy has long been assumed to be an adaptation to avoid predators, as the natural reaction of most larks to predators is to crouch and hide (de Juana *et al.* 2004, Dean & Williams 2004). However, the processes by which larks come to take on the colour of their surroundings have not been identified. Archer and Godman (1961) made reference to Gloger's Rule in this regard, and indeed looking across the larks it is possible to find examples, both within and between species, of a positive relationship between rainfall and plumage colour saturation, conforming to Gloger's Rule, which also follows patterns in soil colour; larks of arid areas tend to be paler than larks of more mesic habitats. Extreme examples include the very dark White-tailed Lark *Mirafra albicauda* of wet tropical Africa and the very pale Gray's Lark *Ammomanopsis grayi* of the ultra-arid Namib. Similarly, the subspecies of many southern African larks, such as Pink-billed Lark *Spizocorys conirostris* and Spike-heeled Lark *Chersomanes albofasciata*, are darker in the wetter east than in the more arid west (Macdonald 1953, Hockey *et al.* 2005, Peacock 2012). However, Gloger's Rule is descriptive rather than mechanistic, and rainfall may be the ultimate driver of a more proximate relationship between plumage and soil colour; White-tailed Lark is largely confined to very dark vertisols (black cotton soils), which only form in areas of high rainfall, and Gray's Lark inhabits pale quartz gravels, which contain little dark organic matter due to low rainfall. Thus rainfall influences soil colour through the known relationship between rainfall and soil organic content; however, this does not elucidate the mechanisms by which soil colour influences lark colour. Furthermore, Gloger's Rule cannot explain the wide variation in lark coloration that can occur across equally arid regions, as illustrated by the example of the Desert Lark cited above.

Individuals that differ in colour from their substrate may suffer higher rates of predation, leaving the colour-matching individuals and their presumably colour-matching offspring to predominate on a particular substrate. Such a process has been demonstrated in *Peromyscus* mice in Florida, where there is a strong selective advantage for mice that match the colour of their local background substrate (Vignieri *et al.* 2010). A process of natural selection on plumage colour might be expected to lead to disruption to gene flow between

populations of the same species on different substrate types and, by implication, to rapid speciation, as the dark offspring of dark larks would themselves be restricted to dark soils, thus isolating them from pale forms of pale substrates. The genetic isolation that might arise from segregation by soil type was recognized over half a century ago (Macdonald 1953). However, there is no evidence of deep genetic divergence between adjacent populations of different colours. For example, Desert Larks of the very dark subspecies *Ammomanes deserti annae*, which inhabit black lava deserts in Jordan, are indistinguishable on the basis of variation in the mitochondrial cytochrome b gene from the pale sandy subspecies *Ammomanes deserti isabellina* of southern Jordan south to Saudi Arabia and the Nile Valley, whereas there are deep genetic divergences between these two forms and taxa of intermediate colours occurring elsewhere (Alström *et al.* 2013). A lack of divergence between phenotypically very different forms could be due either to separation that is too recent for overall genetic differences to have evolved, or to homogenization due to interbreeding. In either case, it is possible that there has been strong selection on a few plumage colour genes while the rest of the genome has not changed much, or that there has been strong selection on a few plumage colour genes while the rest of the genome has been more permeable to introgression than those colour genes (cf. Poelstra *et al.* 2014, Toews *et al.* 2016, Vijay *et al.* 2016). As pointed out by Zink (2004), there is a generally poor correlation between subspecies rank and evolutionary diversity.

Substrate colour, then, may not necessarily act as a barrier to gene flow. This permits the intriguing possibility that the colour of an individual lark is not fixed for the duration of its lifetime, but is plastic with respect to the colour of its environment. There are at least two mechanisms by which this could happen. First, larks may achieve camouflage through a process of environmental 'cloaking', whereby birds absorb or adsorb colourants or particulates from the substrate and thereby come to take on its colour. This possibility was first suggested by Kleinschmidt, repeated by Bannerman (1927) and Niethammer (1940), and developed further by Mayr and McEvey (1960). The use of natural colourants to stain plumage is not unknown in birds. Sandhill Cranes *Grus canadensis* and Bearded Vultures *Gypaetus barbatus* dye their feathers with iron-rich soils to give them a characteristic rich orange-brown coloration (Nesbitt 1975, Negro *et al.* 1999). Male Rock Ptarmigans *Lagopus mutus* stain their white winter plumage brown when it becomes conspicuous after snow-melt (Montgomerie *et al.* 2001). Cosmetic coloration using exogenous sources such as soils may be more common in birds than is currently recognized (Delhey *et al.* 2007). During our handling of museum specimens of larks, we have sometimes been able to detect soil staining, visible

through a microscope as tiny particles on the feathers, and be able to wash it off with water and soap, with a resultant change in plumage colour. Environmental cloaking may be linked to the habit of many larks to dust-bathe (de Juana *et al.* 2004). Whether the microstructure of lark feathers, particularly those of the dorsal tracts, are adapted to allow larks to adsorb colorants from their local environment is unknown, but such an adaptation could solve the problem of avoiding predators without preventing dispersal into areas with substrates of very different colours. It could also set the stage for genetic evolution by allowing initial persistence in new environments, with phenotypic plasticity laying the path for genetic adaptations (Price 2006, Pfennig *et al.* 2010).

A second possible mechanism of individually adaptive substrate colour-matching is that larks are capable of altering the colour of their feathers during moult in response to environmental stimuli, for example by changing the ratio of eumelanin to pheomelanin (McGraw *et al.* 2005) or by modifying feather microstructure, in ways analogous to the production of melanin (tanning) in response to UV in humans. Although the expression of melanin-based plumage colour is thought to be less phenotypically plastic than the expression of carotenoid-based coloration (Roulin & Ducrest 2013), melanization in birds is known to be affected by a range of factors, including hormone production, environment and social conditions (Price 2006). Thus it might be possible that dark larks settling on a pale substrate could, at their next moult, produce feathers with a lower concentration of eumelanin, a different distribution of melanin granules (van Grouw 2017) or a different feather microstructure, giving them a paler appearance. Plumage coloration appears to be under the control of a very small number of genes (Toews *et al.* 2016), perhaps increasing the feasibility of epigenetic alteration of plumage colour. Our understanding of the ability of organisms to modify gene expression in response to environmental stressors, with resulting changes in phenotype, is in its infancy, but already it is becoming apparent that this may represent a significant source of variation in a number of traits (Fresard *et al.* 2013), including plumage pattern and colour (Jiang *et al.* 2004).

Taxonomic implications

Further work, perhaps including experiments on birds in aviaries, the microscopic examination of feather structure or examination of colour changes after the washing of feathers, will be required to explore and test these various options, and other plausible explanations (perhaps involving diet, although this appears to have little influence on melanins) could no doubt be proposed. However, it is interesting to note that at least some of the

mechanisms proposed above would permit non-permanent associations between plumage coloration and substrate within individuals. Phenotypic plasticity in adapting the plumage to local conditions, suggested by Guillaumet *et al.* (2005) to be a driving force in the evolution of variation in *Galerida* larks in North Africa, may therefore act at the level of individuals as well as populations. This has implications for taxonomy at the level of subspecies, as in the great majority of type descriptions of subspecies of larks, general plumage tone is the main, and indeed often the only, character on which the subspecies are proposed (de Juana *et al.* 2004). Furthermore, there is a presumption against giving the same subspecies name to almost identical but widely allopatric forms (Mayr & McEvey 1960), further increasing the number of proposed subspecies in some particularly variable species. However, if general plumage colour is temporally plastic within individuals, then it is of questionable use as a taxonomic feature, rendering untenable many subspecies as currently proposed using a system of trinomial classification. This problem was recognized by Ernst Mayr, who proposed the term 'ecophenotypic' to describe the colour attributable solely to soil staining, and suggested that 'ecotypic' variation, i.e. that due to the selective effects of the local environment, is that which can be attributed to the colour remaining after the soil particles have been removed (Mayr & McEvey 1960). However, Mayr also pointed out that it could be equally well argued that *all* processes that lead to substrate colour-matching, including dust-bathing to attain extrinsic coloration, are fundamentally selective and therefore 'ecotypic'. Whether a single behavioural adaptation, such as dust-bathing, or a single physiological adaptation, such as a feather structure that enables the capture of coloured dust, if found across all populations of a species, would justify a plethora of trinomials is open to debate. Instead, it might be better to dispense with traditional trinomials for such cases and to follow Mayr and McEvey (1960) in referring to different colour forms as polytopic 'substrate types'.

We suggest that substrate colour-matching in larks might be a useful model for developing a deeper understanding of intraspecific variation and phenotypic plasticity in birds and could identify and clarify patterns of phenotypic variation that cannot satisfactorily be explained by local adaptation of heritable traits alone. This casts further doubt on the relevance of traditional trinomials to describe the outcome of adaptive phenotypic plasticity.

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