Adaptive plumage wear for increased crypsis in the plumage of Palearctic larks (Alaudidae)

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Larks (family Alaudidae) are ground-dwelling passerines living in open habitats with sparse vegetation, i.e., deserts, grasslands, and agricultural fields. A majority of species occur in Africa and Eurasia. Lark species, about 100 in total, are mostly dull colored with a predominance of beige and light brown coloration, and/or streaked patterns due to melanin pigments, with an absence of bright and conspicuous carotenoids and/or structural blue or iridescence. There is no obvious sexual dichromatism in a majority of species (Cramp 1988), except a few species, including the *Eremopterix* genus and the Black Lark (*Melanocorypha yeltoniensis*), where males are much darker than the females, and the *Eremophila* species, in which males have longer head horns.

Their general appearance has made larks a textbook example of cryptic species in the avian world (Cramp 1988). The reasons underlying their extreme dependence on camouflage seem to be that they are generally small and defenseless, and that they breed solitarily on open nests on the ground, this making them vulnerable to attacks by avian predators, as well as carnivore mammals and reptiles (Dean and Williams 2004). They are, however, very confident in their crypsis and, for instance, they would leave the nest only at the last moment when approached by a potential predator including humans (Cramp 1988).

Most larks molt the juvenal plumage completely soon after they fledge (Cramp 1988), which is rather unusual

among passerines (Kiat and Izhaki 2016), and are among the few songbirds in which adults undergo a single post-breeding molt, typically at the end of the summer (Svensson 1992). There are some exceptions to this rule, and, for instance, Vaurie (1951) suggests that two to five out of 27 Asian species of larks may undergo a double annual molt. Nonetheless, a majority of Palearctic larks (and perhaps African ones too, although precise data are lacking) initiate their aerial courtships in spring with a highly worn plumage, and they actually breed and raise their young in the most worn state of the plumage before the next molt. The Collins Bird Guide (Svensson et al. 1999), a comprehensive identification guide for the birds of the Western Palearctic, includes different illustrations for the autumn (fresh) and spring (worn) plumages of 15 out of the 20 lark species covered by the guide. Only 10 other species of different families are shown in fresh and worn plumages out of about 700 species covered in the guide. Most songbirds follow a different strategy from the larks and start breeding in rather prime plumage condition, many of them having previously undergone the prealternate molt, involved in the formation of a fresh, attractive plumage thought to be sexually selected for mate acquisition (Gualler and Figuerola 2016).

The Thekla's Lark (*Galerida theklae*) in the left panel of Fig. 1 was photographed on 25 February 2018 in central Spain. It was midway between its last full molt, which possibly had taken place in late August–September 2017, with the next one scheduled for late summer 2018. If the bird bred, it would do so no earlier than May 2018, and thus no less than 2–3 months after the picture was taken. The plumage of the bird is very worn, and this is particularly evident in the three tertial feathers covering the primaries and secondaries on both wings. These tertials have been reduced to one-half their original length, their margins are also abraded in a random fashion, and even the color of their outer margin is bleached in relation to the central vane of those feathers. In addition, there is evidence of feather wear in the tail feathers and upper tail coverts. By comparison, a Thekla's Lark with a freshly molted plumage in September would show a light-colored fringe in all covert feathers and tertials (Fig. 1, right panel).

To establish the feather wearing pattern of larks in low latitudes of the Western Palearctic, we examined 73 different specimens in the Bird Collection of Doñana Biological Station, collected in Spain or Morocco, and belonging to nine different lark species, including 27 adult Thekla's Larks (Appendix S1: Table S1). We noted whether there was wearing of the tertials, the largest feathers visible on the back of larks, as well as the date of capture for every specimen. As a control, we checked feather wearing in four passerine species that share open

FIG. 1. Thekla's Lark (*Galerida theklae*) displaying a worn plumage photographed on 25 February 2018 in central Spain (left panel). The feathers in the back are heavily damaged but may provide disruptive camouflage. This individual is midway between its last full plumage molt in August–September and the next one in the same period. The arrow points to the central tertial feather of the right wing. The Thekla's Lark on the right was photographed on 18 September 2017 in southern Spain, soon after completing its post-breeding molt. The light-colored fringes of the tertials, and in fact of all covert feathers, appear intact and fresh. Photo credits: Juan J. Negro.

habitats with different species of larks, present a similar brown/beige camouflaged coloration, and were available in the Doñana collection: three species with a single annual molt (i.e., *Miliaria calandra* [Emberizidae], *Passer montanus* and *Petronia petronia* [Passeridae]), as well as *Anthus pratensis* (Motacillidae), with two annual molts. We have also included the Bearded Reedling, *Panurus biarmicus*, the only extant species in Panuridae, the likely sister-group of Alaudidae (Selvatti et al. 2015), which also undergoes a single annual molt and is associated with reed beds.

We concluded that larks of the species sampled presented a heavily worn plumage across most of the annual cycle, from November to at least June. All adult birds with new tertials had been collected in just four months: August to November. However, 12 out of 17 lark specimens captured in November already presented worn tertials. In fact, this wearing pattern was previously suggested in Cramp (1988), who described consistent differences in the freshly molted autumn feathers of all 21 lark species in the Western Palearctic compared to their worn spring plumage. For a majority of those lark species, Cramp (1988) reported bleaching and wear of the whole plumage soon after completion of the molt in September. By contrast, the non-lark passerines in our sample, including the closely related Bearded Reedlings, presented fresh and unworn tertial feathers across the year. It thus

remains paradoxical that larks with a damage-prone plumage undergo a single annual molt. The latter is typical of seasonally homogeneous areas, whereas a biannual molt is typical of temperate latitudes with cold winters and hot summers: precisely the environmental conditions experienced by a majority of Palearctic larks (Beltran et al. 2018). Larks belong to a phylogenetic clade within the Passeriformes, the Sylvioidea (Selvatti et al. 2015), that concentrates species with a single annual molt (e.g., *Cisticola juncidis*, *Acrocephalus melanopogon*, *Panurus biarmicus*, *Aegithalos caudatus*). Outside the Sylvioidea, the species known to have a single annual molt in the Palearctic are all the Sturnidae, the Passeridae, *Miliaria calandra* in Emberizidae (Svensson 1992), and *Pyrrhula pyrrhula* and *Carduelis flammea cabaret* in Fringillidae (Beltran et al. 2018).

We built a phylogeny with all the species in Appendix S1: Table S1, plus other lark species of the different main clades recently recognized (Alström et al. 2013), as well as the species with a single annual molt mentioned above, and representative passerines with a biannual molt. A single annual molt and a rapidly degrading plumage may be exclusive (according to current knowledge) to some larks (Appendix S1: Fig. S2).

Under a light microscope (10–20× magnification), we observed that the distal portion of the barbs of newly molted tertials or covert feathers lack structurally

reinforcing melanin, and the barbs are not closely entwined by the barbules. In addition, the tips of a majority of the barbs are already broken even in fresh feathers (Appendix S1: Fig. S1, Fig. 2S, Supporting information). Therefore, larks run counter to the prediction that bird species will produce a more durable plumage when this plumage will be used for longer than in species that replace it more often by means of prealternate molts (Kiat and Sapir 2018).

The plumage coloration of larks is said to exemplify background matching (e.g., Donald et al. 2017). The pressure for optimal background matching is so intense in larks that a significant plumage darkening in response to a shift to new agriculture soils has been reported for the only lark species breeding in North America, the Horned Lark *Eremophila alpestris* (Mason and Unitt 2018), which incidentally counts no less than 42 subspecies subtly varying in color.

However, larks may have gone a step further to camouflage themselves on the open ground: by having randomly broken tertials and remiges, as well as covert feathers, they also acquire a form of structural camouflage, on top of background color matching, known as disruptive camouflage. This type of camouflage was already recognized early in the 20th century by Thayer (1909) who defined it as the patterns that break up the appearance and body outline. This form of camouflage has gained attention in recent years, particularly after its adaptive value was demonstrated experimentally (Stevens et al. 2006).

Tertials, and possibly all covert feathers in the plumage of larks, break and wear rapidly due to their intrinsic fragility, as their fringes are unmelanized, facilitated by increased abrasion at ground level (Jenni and Winkler 1994), and also with the help of the sand and dust baths at which larks are so adept. Dusting is uncommon in passerines, except for the larks and the sparrows in the family Passeridae (Simmons 1959). Larks live with worn feathers most of the year, even though a damaged plumage may compromise bird flight (Swaddle et al. 1996), and therefore, we propose it may actually be an adaptive trait. Disruptive markings have been predicted to be distributed so as to break up each of the animals' body parts (Stevens and Merilaita 2009). The Thekla's Lark in Fig. 1 also features an erectile crest of about the length of the beak, a few bristles under the beak itself, and some downy feathers protruding on both flanks of the bird. All these features and posture help in disrupting the contour of the bird, being commonplace in larks. Out of 20 species of larks in the Western Palearctic, 11 have erectile crests in both sexes (Svensson et al. 1999) that may contribute to break up the head outline, perhaps like the feather tufts in some cryptic owl species (Perrone 1981).

We propose that lark species combine at least three different camouflage mechanisms (Stevens and Merilaita 2009) to hinder their detection by predators and enhance survival.

- 1) Background matching for soil and dry vegetation to the point that the frequent color polymorphisms within species (e.g., Cramp 1988) reflect differences in soil coloration (Mason and Unitt 2018).
- 2) Disruptive camouflage provided by worn feathers most of the year, by creating internal edges in a random pattern, and thus cancelling out the effect of smooth lines seen in fresh feathers soon after the molt. In fact, the tertials of the larks, where the wearing is more evident, are larger than in most species of Passeriformes, and partly cover the flight feathers when the bird is perching or marching on the ground. Disruptive patterns may exploit edge detectors in predator vision and hinder detection of camouflaged prey (Stevens and Merilaita 2009). In this sense, larks may have turned need into a virtue: they possibly cannot avoid a premature damage of their fragile plumage, and instead of incurring the cost of molting repeatedly, they gain the advantage of a form of camouflage different but complementary to background matching.
- 3) Behavioral adaptations for camouflage (Stevens and Ruxton 2018): by erecting the crests and often fluffing the plumage when perching, or crouching on the ground when alarmed, the outline of the lark as a typical passerine is further distorted, presumably making detection even more difficult.

Our research on Palearctic larks raises the question whether lark species living in other areas present rapidly wearing plumages. A majority of lark species live in seasonally changing environments and plumage degradation over time may help them adapt to seasonal changes in background coloration. Survival estimates for larks through the year are sorely lacking, but the only species with data (Vögeli et al. 2008), the Dupont's Lark *Chersophilus duponti*, had the same survival probabilities in the breeding and post-breeding periods. In other words, the worn plumage at breeding does not hinder survival for at least this lark species. Further studies are, however, needed to determine if this is true for the remaining Alaudidae. Our phylogeny suggests that at least one *Calandrella* species secondarily gained a prealternate annual molt. A closer look to the *Calandrella* genus and their ecological requirements and behavior is warranted to understand the evolution of the dual trait combination (worn feathers and single annual molt). Last, and if all is equal, it remains to be studied why most larks retained the prebasic molt instead of the prealternate molt, that would allow for a fresh breeding plumage.

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