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IDEA

An avian equivalent of make-up?

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Abstract

We report that a long-distance migrating shorebird, the red knot, makes a complete switch from commonly occurring monoester preen waxes to a much rarer class of higher-molecular-weight diester waxes at the time of take-off to the high arctic breeding grounds. The cold arctic climate would have required a lowering of wax-viscosity, and thus, a shift in the reverse direction. We propose that a sexually selected need for a brilliant plumage has lead to this conter-intuitive temporary shift from monoesters to diester waxes. The difficulty of application of the diester preen waxes under cold conditions would ensure the reliability of the quality-signalling function of this most probably sexually selected trait.

Keywords

Annual cycle, Arctic, *Calidris canutus*, mate choice, migration, plumage quality, preen wax, sexual selection, shorebirds, uropygial gland

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In late May and early June, when red knots *Calidris canutus* take-off on 3000–5000 km long journeys to their high arctic breeding grounds from refueling areas near New York, Reykjavik, Hamburg and Beijing, they trade the congenial climatic conditions of temperate zone coastal wetlands for the extreme chilliness of the still frozen and snow covered tundra deserts bordering the Arctic Ocean (Piersma & Davidson 1992; Wiersma & Piersma 1994; Harrington 1996). The birds depart with body masses of over 200 g, of which they loose at least a third during the nonstop flight.

Although the abrupt changes in environmental conditions encountered by avian migrants may be matched by relatively fast metabolic adjustments (Gwinner 1996; Piersma 1998), nothing comes close to the amazing shift in waxes produced by the preen gland that we have discovered in red knots. Preen waxes, secreted through a small feathered 'nipple' by a special subcutaneous gland on the rump, are actively distributed over the plumage during the birds' preening movements. The secretions usually consist of a mix of monoester waxes, and may function in keeping feathers supple and strong (Stevens 1996). The speed and completeness of the change from lower-molecular-weight monoester waxes, to high-molecular-weight diester waxes within 1 week is remarkable. If anything, we would have predicted a shift in the reverse direction to adjust the preen wax viscosity to cope with the cold Arctic climate.

MATERIALS AND METHODS

Preen waxes were harvested by massaging the nipple or by extracting feather samples. The composition of intact waxes of red knots was determined with capillary gas chromatography-mass spectrometry, as reported in detail elsewhere (Dekker *et al.* 1999). We examined 23 captive red knots belonging to the population wintering in western Europe and breeding in northern Greenland and the Canadian high-arctic islands (subspecies *islandica*, Piersma & Davidson 1992), nine of which were followed throughout the period of northward migration. In addition, the preen waxes of 17 birds were sampled in May 1998 in Delaware Bay, U.S.A. These birds belonged to the subspecies *rufa* wintering in Tierra del Fuego and breeding in the lower Canadian Arctic (Harrington 1996). Finally, a single *islandica* bird collected in June 1990, a week after arrival on the breeding grounds near Alert on Ellesmere Island, Canada, was examined.

RESULTS

Throughout the year the preen waxes of the red knot were dominated by C_{21}–C_{38} monoesters composed of C_7–C_{16} 2-methyl and 2,6-, 2,8- and 2,10-dimethyl fatty acids esterified with C_{11}–C_{22} straight chain and methyl-branched alcohols. However, in late May, red knots that were kept in aviaries, but that nevertheless maintained their natural mass and moult cycles (see Piersma *et al.* 1995), made a complete shift towards the production of

C_{32}–C_{46} diesters composed of C_{12}–C_{18} alkane-1,2-diols esterified with C_8–C_{18} straight-chain fatty acids (Fig. 1a–b). As soon as their body masses dropped (i.e. as captive birds give up northward migration and a breeding attempt), they reverted to producing monoesters. Despite intensive searches (Jacob 1992), the particular class of diester waxes (Kolattukudy 1972; Saito & Gamo 1972) has not been found in the avian Order Charadriiformes before.

The rapid shift from monoesters to diesters was confirmed for red knots staging in Delaware Bay, U.S.A. Birds were sampled in early May, immediately after their arrival from Argentina and Brazil, and just before their departure for the Arctic (Piersma & Davidson 1992; Harrington 1996). Only the heaviest birds from 28 May, one or two days before departure, showed the shift to diester waxes (Fig. 1c). This demonstrates that diesters are not linked to 5000–8000 km long flights from South to North America, and confirms that the transition takes place in a matter of days. Feathers of a mated female carrying half-complete egg follicles, sampled on 6 June 1990 on the tundra near Alert, Ellesmere Island, Canada, showed only faint traces of diester waxes. Thus, production of high-molecular-weight diester waxes only occurs during the brief period of flight towards and the arrival on the tundra breeding grounds.

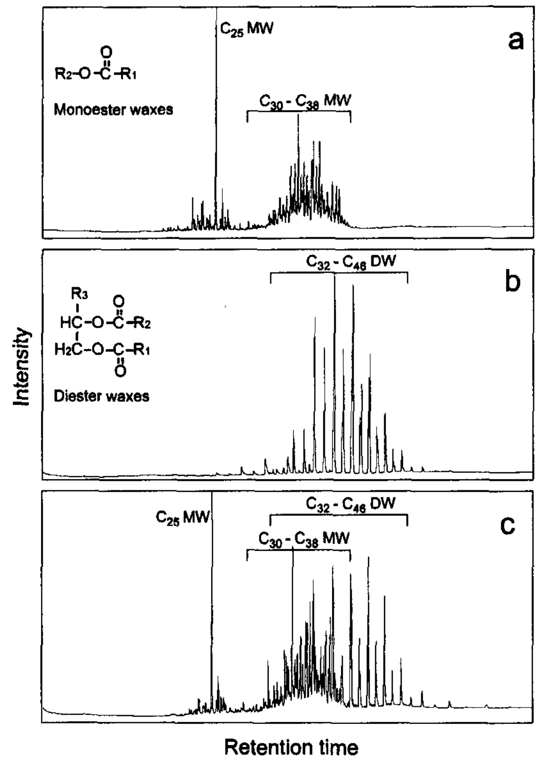

Figure 1 (a–b) Examples of the gas chromatograms of the succession of preen waxes produced by captive red knots (in this particular case bird #387 on 19 May and 2 June 1998), showing the complete shift from monoester waxes (MW) to diester waxes (DW). (c) Example of the preen wax composition of a female red knot (#23) in Delaware Bay on 28 May 1998 (1–2 days before departure to the Arctic), indicating a mix of the two wax types. Red knots from this population with lower body mass values (i.e. not ready for departure) showed preen wax compositions as indicated in (a).

DISCUSSION

Upon arrival on the tundra not only do cold conditions prevail (Wiersma & Piersma 1994), but mate choice takes place within the first few days as well (Whitfield & Brade 1991). During mutual mate assessment (Jones & Hunter 1993), the quality of the plumage of potential partners may be of decisive importance (Piersma & Jukema 1993). We do not believe that diester waxes act as substrates for pheromones (Kolattukudy *et al.* 1987), as small volatile molecules that would result from hydrolysis of diesters could not be detected on feathers. Instead, we propose that a sexually selected need for a brilliant plumage in both sexes might determine the temporary shift from monoesters to diester preen waxes. As it is difficult to apply under cold conditions, only in biochemically and behaviourally adept individual red knots could the congealed diester waxes generate the type of plumage-shine with which Frisian egg-collectors identify lapwings *Vanellus vanellus* in heat (J. Jukema, personal communication). As shown before (Bennett & Cuthill 1994), there may be much more to avian beauty than meets the human eye.

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BIOSKETCH

TP maintains research interests in behavioural ecology, ecophysiology and marine ecology using field and indoor experimental approaches, with one focus on the annual cycles, long-distance migrations and energetics of shorebirds and another on intertidal foodwebs.

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