Synthesis

The migrations and annual cycles of five subspecies of Knots in perspective

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To summarize the migration patterns and annual cycle characteristics of Knots, we recognize five subspecific groups (*islandica*, *canutus*, *rogersi*, *roselaari* and *rufa*) on the basis of genetic, morphologic and behavioural evidence. The 'wintering' areas for all except *roselaari* have been identified. All Knots breed in the High Arctic, but they 'overwinter' from 58°N to 50°S, migrating to the corners of all continents. The largest populations (350,000 - 500,000 birds), representing the most numerous subspecies *islandica* and *canutus*, 'overwinter' respectively in western Europe and western Africa. The smaller populations of *rufa* 'winter' in Patagonia/Tierra del Fuego, and of *rogersi* in Australia and New Zealand. All subspecies undertake long-distance flights of 2,000 - 6,000 km, often completely over water. *Islandica* makes the shortest flights but crosses the Greenland icecap. The two trans-equatorial migrating subspecies *rogersi* and *rufa* make more long-distance flights per season and carry their breeding plumage for longer periods than *islandica* and *canutus*. The great variation in non-breeding latitudes means that the various 'wintering' populations are exposed to different and sometimes rather erratic photoperiodic regimes, suggesting that Knots generally rely on endogenous timers to organize their year. In spite of the migratory differences, birds of the *islandica* and *canutus* subspecies wintering in the northern hemisphere can achieve their migratory patterns with the same basic endogenous circannual regime.

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INTRODUCTION

Knots *Calidris canutus* are high-arctic breeding waders and long-distance migrants, wintering in large concentrations in certain coastal wetland areas, roaming the intertidal flats in search of invertebrate (usually mollusc) prey. Yet, with this brief summary of Knots as a species, their uniformity stops. The five currently recognized subspecies show great diversity in breeding and 'wintering' latitudes, and consequently in the migration distances flown to get from one area to the next.

In this chapter we aim to summarize both the uniformity and the diversity of the migratory patterns and the associated annual cycle characteristics of the five identified subspecies of Knots. Much of the chapter will be admittedly speculative and based on poorly tested hypotheses. We hope, however, that this exercise of synthesizing information from the many other papers in this volume will highlight the gaps in our understanding of the migration of this exciting species, as well as identify the research lines beyond. We also hope that the comparative approach adopted here can be applied between and within other migrant waders.

ASSIGNING SUBSPECIFIC GROUPS: CUTTING A GORDIAN KNOT?

Although Knots form an ancient (4-6 million years old) wader lineage, this has not lead to an accumulation of genetic variation, probably as a result of repeated population bottlenecks (Baker 1992). In spite of the low overall genetic variation measured by gel electrophoresis of neutral allozymes, there exists significant genetic variation between different stocks of Knots (Baker 1992). The available evidence from a small series of sequencing data of mitochondrial DNA (mtDNA) suggest that *rufa* and *rogersi* split only about 30,000 years ago, and *rufa* and *islandica* 85,000 years ago (Baker 1992). The current subspecies are therefore late Pleistocene products.

Authors have taken their time in describing the subspecies of Knots. After identifying Knots as a species (Linneaus 1758), Linnaeus described the *islandica* subspecies in 1767, *rufa* was described by Wilson in 1813, *rogersi* by Mathews in 1913 (see Cramp & Simmons 1983) and *roselaari* by Tomkovich in 1990, and there has been disagreement about the number and the names of the subspecies all along. It will come as no surprise that this discussion is far from finished today. One may wonder 'what's in a name?', but it is helpful to assign accurately Knots occurring in an area to specific and more or less isolated breeding and wintering populations, if such populations existed. Accurate assignments of identifiable and closed biogeographical populations (which we can call subspecies for morphologic and/or genetic reasons) not only help research into the biological reasons of the variety of migratory tactics among Knots, but also the development of effective conservation programmes (for the latter see Davidson & Piersma 1992).

We have tried to summarize the most recently published points of view about the taxonomy, subspeciation and relatedness of different populations of Knots in Figure 1, also trying to compress the different views into a common frame. In view of their uncertain (migratory/breeding) status (A.J. Baker pers. comm.) we have excluded the conflicting data presented by Baker (1992: Figure 3) on the mtDNA characteristics of birds from Alaska in the following descriptions of subspeciation in Knots.

Roselaar (1983) resurrected subspecific status to the European-wintering/Nearctic-breeding *islandica* population as separate from the African-wintering/-Siberian-breeding *canutus*, thereby recognizing four subspecies. Roselaar indicated, moreover, that the birds from Wrangel Island and Alaska might also be sufficiently distinct to qualify for subspecific status. Tomkovich (1990, 1992) with more material available confirmed Roselaar's suggestion, naming the Wrangel/Alaska birds *roselaari*. In contrast to Roselaar, Tomkovich was, however, unconvinced about the morphological differences between *islandica* and *canutus* and indicated that there is considerable variation within *canutus*. In our view birds currently called *canutus* may be an assemblage of three quite separate breeding populations in Taymyr, the Yakutsk region and the New Siberian Islands, respectively.

Nobody knows for certain where the breeding birds from Wrangel Island and north-west Alaska 'winter', nor how they get to and from their wintering grounds. Tomkovich (1992) suggested a route along the western seaboard of North America. No great concentrations are known from this area, but a few 10,000s of Knots do winter in a few sites in middle

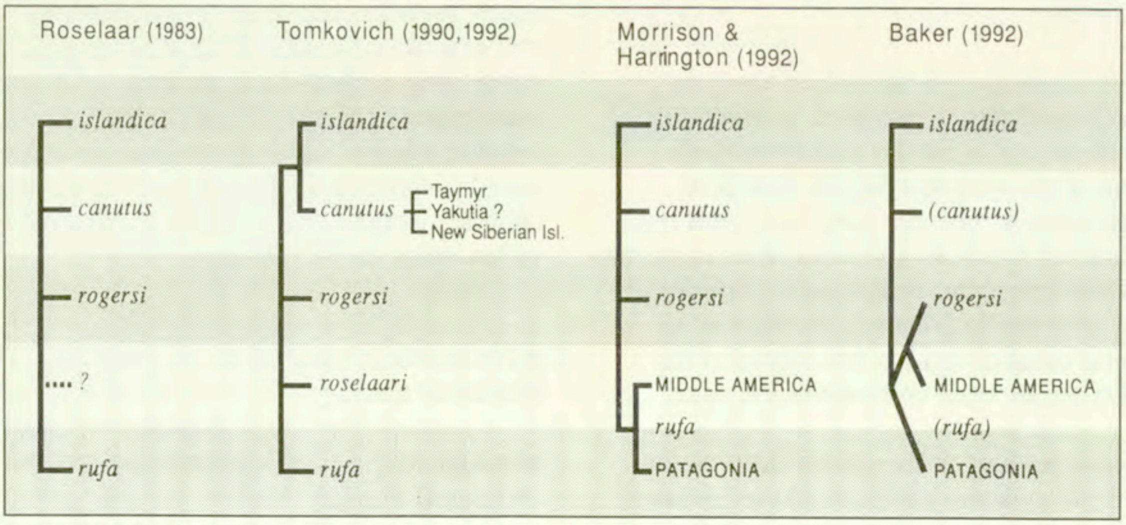

Figure 1. Classification of Knot populations according to different recent authors. Baker (1992) gives degrees of genetic diversication (without examining material from *canutus*) whereas the remaining authors give simple classifications, hence the variations in 'tree' structure.

America. Although Morrison & Harrington (1992) assign the population wintering in Florida to the *rufa* subspecies, they do indicate the distinctiveness of this group from the majority of '*rufa* proper', i.e. the birds that 'winter' in Patagonia/Tierra del Fuego (see Harrington *et al.* 1988). In his Figure 2, Baker (1992) shows that Florida birds clustered with Australian *rogersi* and were different from Quebec and Argentinian *rufa*. In Figure 3 of Baker (1992) the birds from middle American wintering sites (Florida and Texas) are alike and cluster again closely to Australian birds. We feel that the least conflicting hypothesis available at present that brings the various lines of evidence together, is the suggestion that the middle American birds are in fact wintering *roselaari* Knots. The subspecies *rogersi* and *roselaari* breed next to each other, cluster genetically and they may therefore be close relatives and recently diverged subspecies.

Excluding the data from the Alaskan birds, the separation of different groups of Knots on currently available morphological and genetic evidence is thus fairly straightforward. Figure 1, and the literature on which it is based, suggest the species to be an interesting mix of reasonably distinct subspecies, as well as incipient subspecies. The assembled information even hints at an hypothesis about the evolutionary tree of Knots. If we accept the time since separation of *rufa* from *rogersi* at 30,000 years and from *islandica* at 85,000 years (Baker 1992), we can compare these figures to the location of the three arctic breeding areas (see Figure 3). The breeding areas of *rufa* and *rogersi* are very close to each other (with only the breeding area of *roselaari* wedging in) and the time since separation relatively recent, both suggesting a recent divergence. This contrasts with *rufa* and *islandica* which have very close or overlapping (Godfrey 1992) breeding ranges but which separated much longer ago.

The emerging pattern can be interpreted as a circumpolar ring of subspecies where *rufa* and *islandica*

Figure 2. Quantitative 'wintering' distribution of Knots over the globe. The zrea of the circles indicates the non-breeding numbers, the largest dot on the west African coast representing 364,000 birds. Note that the world is well covered with counting efforts as far as the, always coastally occurring, Knots are concerned. Only for north-east Australia (the inaccessible Gulf of Carpentaria) are non-breeding numbers are really unknown. This figure was compiled from: Morrison & Ross (1989); Morrison & Harrington (1992); Smit & Piersma (1989); Davidson & Wilson (1992); Piersma *et al.* (1992); Lane (1987) and Barter (1992).

would be the opposing ends of lines of diverging from an ancestral mid-Siberian Knot stock (perhaps closely related to what we recognize as *canutus* today). The genetic make-up of the Siberian breeding populations should be compared with that of the other groups in order to test this. If confirmed, the hypothesis may suggest that the northerly wintering habit of *islandica* Knots is the most recent innovation in Knot biology.

In the descriptions that follow we stick to the five most distinct groups (or populations or subspecies): *islandica*, *canutus*, *rogersi*, *roselaari* and *rufa*.

THE NON-BREEDING DISTRIBUTION

The worldwide non-breeding or 'wintering' distribution is intriguingly uneven (Figure 2). ('Wintering' is usually put in quotes in recognition of the fact that the northern hemisphere Knots often experience southern hemisphere summers when not breeding.) Although we view Knots as typically tropical 'winterers' (see above), the largest numbers are found not only in in western Africa but also in western Europe. Other sizeable concentrations are found in Patagonia/Tierra del Fuego, northern Australia and New Zealand.

The winter distribution of Knots far from reflects the availability of intertidal flats in benign climates, since in such cases large concentrations would be expected also along the western shores of the Americas, the coast of the Guianas in South America, along the east African coastline, in the Arabian Gulf area and in south-east Asia. Only throughout the East Atlantic Flyway (Piersma *et al.* 1987; Smit & Piersma 1989) do Knots occur broadly in proportionality to the available mudflat areas. Does this mean that the unoccupied coastal areas therefore cannot generally support Knots? And what might the constraints be (climate, availability of mollusc prey, competition with other species)?

The Guiana coasts have a benign winter climate and can support Knots since the area is used during stopovers by migrating *rufa* 'wintering' in southernmost South America, at least during southward migration (Morrison & Harrington 1992). There is apparently something about the food supply along the Patagonia/Tierra del Fuego coast that attracts the available Knots to spend the 'winter' there, but this has yet to be studied. Curiously, very few Knots fly either over the Mediterranean area, east Africa or west Asia (Summers *et al.* 1987a; Underhill *et al.* 1989; Zwarts *et al.* 1991), but in this context their absence in winter in e.g. the Arabian Gulf is expected.

The delta of the Yellow River near Shanghai, China, and the extensive mudflats along the Korean coast are used during migration (Long *et al.* 1988; Barter 1992) but are probably too cold in winter. Perhaps we would expect more Knots to winter in the Indonesian and Philippine archipelagos, but they do not. Could their absence, and the relatively low total population size of *rogersi* (Table 1), be related to the very high hunting pressure on waders in this part of the world (Parish & Howes 1990; C. Swennen pers. comm.)?

Numbers of *rufa* are also much smaller than those of *canutus* and *islandica*. In fact, *rufa* populations might still be recovering from the hunting pressures on waders of the late 19th and early 20th century in e.g. New England and the Maritime provinces of Canada (Gollop *et al.* 1986). Yet, there is evidence that they have again been declining between 1972 and 1983 (Howe *et al.* 1989). The possible reasons need more comprehensive analyses. In such evaluations the size and quality of the breeding as well as the stopover areas need to be taken into account.

With roughly 20,000 birds, *roselaari* may be the rarest subspecies (Table 1), but this population size figure is based only on the approximate numbers wintering in middle America (Morrison & Harrington 1992). If the 110,000 Knots counted by Gill & Handel (1990) on 21 May 1980 in the Yukon-Kuskokwim delta in western Alaska belong to this subspecies, the figure of 20,000 birds for *roselaari* is much too low. But where would all these birds then pass the winter? The only other subspecies to which some or all of these Alaskan Knots might belong would be *rogersi*, in which case this population would have a marked 'dog-leg' in their migration route from east Asia to the Chukotski Peninsula breeding grounds.

MIGRATION ROUTES

Although Knots eventually reach all corners of all continents for 'wintering', they overfly many apparently suitable regions of the world (Figure 3). Knots hardly ever show up on the Pacific coast of South America, along the east coast and in the interior of Africa, in western Asia and on the Indian subcontinent.

Figure 3. Global distribution and migration pattern of Knots. Vertical shading indicates the breeding areas, horizontally striped spots the stop-over areas only used during south- and northward migration, the cross-hatched spots the areas used both as stop-over as wintering sites, and the vertically striped spots designate areas used a wintering areas only. The shaded corridors indicate proven migration routes, the broken shaded corridors tentative migration routes suggested in the literature. Compiled from the information given in the review chapters in this volume.

A few 100 Knots are known to overwinter in the Gulf of Gabes, Tunisia (van Dijk *et al.* 1986), and similar numbers pass through the Porto Lagos area in northeast Greece in March-April (Meininger 1990) and through the Sivash wetlands in the Crimea region during both the north- and the southward migration (Chernichko *et al.* 1991). Since the route from Tunisia over Greece and the Crimea to Siberia is used intensively by other species such as Dunlins *Calidris alpina* and Curlew Sandpipers *Calidris ferruginea*, the Knots encountered in Tunisia, in Greece and in the Sivash region might represent the same isolated group (J. Kube pers. comm.) of unknown subspecific status. This group of Knots would possess the unique feature of only using 'continental/inland' wetlands during their migration.

It is especially remarkable that the Knots 'wintering' in southern Africa do not use the African/west Asian route from and to Siberia. The other Siberian breeding wader species 'wintering' there, such as Curlew Sandpipers, do use these more eastern routes (Elliott *et al.* 1976; Summers *et al.* 1987b; Underhill *et al.* 1989). This route would save the Knots 1,000 - 2,000 km (or *c.* 10 %) of the distance one-way (Dick *et al.* 1987).

The longest overwater flights (5,000 - 6,000 km) are made by *rufa* when crossing the Atlantic from northeast America to South America and by *rogersi* when crossing the easternmost Pacific to and from Australia. (There is the additional possibility that *canutus* 'wintering' in southern Africa bridge the 5,000 km to west Africa across the Gulf of Guinea, Dick *et al.* 1987.) *Islandica* crosses stretches of ocean 'only' half as wide as those crossed by *rufa* and *rogersi*. Most *canutus* fly mainly close to or over land, but they cover long stretches (4,000 - 5,000 km) without stops. The second largest overland flights (*c.* 3,000 km) are probably made by *rufa* when overflying Amazonia between southern Brasil and the Caribbean. There is also a possibility that *rufa* Knots

Table 1. Interpretive summary statistics of population, migration, mass and moult in five subspecies of Knots as delineated in the text, based on information presented in this *Wader Study Group Bulletin Supplement*, and recognizing *roselaari* as a valid subspecies believed to breed in northwest Alaska and on Wrangel and to winter in middle America. The information on non-breeding (N.B.) latitudes, latitudinal (Lat.) and great circle (G.C.) distances between breeding and non-breeding areas are for the major segments of the *canutus* (west Africa) and *rufa* (Patagonia/Tierra del Fuego) populations. The maximum flight distances refer to the currently most likely single long-distance flights made by the different subspecies. The mass and maximum recorded daily mass gains refer to recorded or extrapolated (e.g. mass for *canutus*) population averages. The timing of moult is given as month and the 10-day period (decade) within that month, that the 'average individual' in the main segment of the population has completed half the wing moult (i.e. a primary moult score of 25 in many recording schemes).

Subspecies	Population size (n)	Breed. lat. (°)	N.B. lat. (°)	Lat. dist. (°)	G.C. dist. (km)	Max.flight distance (km)	Mass peak in winter (yes/no)	Spring mass		Wing moult	
								max. mean (g)	max. gain (g/d)	Lat. (°)	Time (m,dec)
islandica	345,000	79N	54N	25	4,500	3,000	yes	205	3.6	53N	S,1
canutus	516,000	67N	17N	50	9,500	5,000	no	210	3.4	17N	S,3
rogersi	200,000	68N	22S	90	12,000	5,800	no	180	?	22S	D,3
roselaari	>20,000?	69N?	20N?	49?	7,000	?	?	?	?	?	?
rufa	125,000	70N	47S	117	10,500	>5,400	?	202	?	47S	D,2

starting in southern Brasil fly in one stage to Delaware Bay, which would imply a single flight of no less than 8,700 km (Morrison & Harrington 1992). It is hard to imagine that they would be able to achieve this without considerable tailwind assistance.

A comparison between the four best known subspecies of Knots (Table 1, Figure 3) clearly indicates that *islandica* is the relatively short-distance migrant amongst the remarkably long-distant flying Knots. Yet it is also the one subspecies crossing a major icecap (on Greenland, Alerstam *et al.* 1986), no mean feat. The immense overwater flights of 3,000 - 6,000 km made by the different subspecies hint at remarkable navigational, or at least orientational, capabilities (Williams & Williams 1990).

ANNUAL CYCLES

A pictorial summary of the timing of annual events in the largest 'segments' of the four best known subspecies of Knots is provided by Figure 4. We have chosen the bi-annual changes in plumage and the timing of the long-distance migratory flights as the important circannual indicators, the latter in view of the extensive nutritional/physiological preparations required. In spite of the considerable differences in wintering latitudes and migration distances (Table 1),

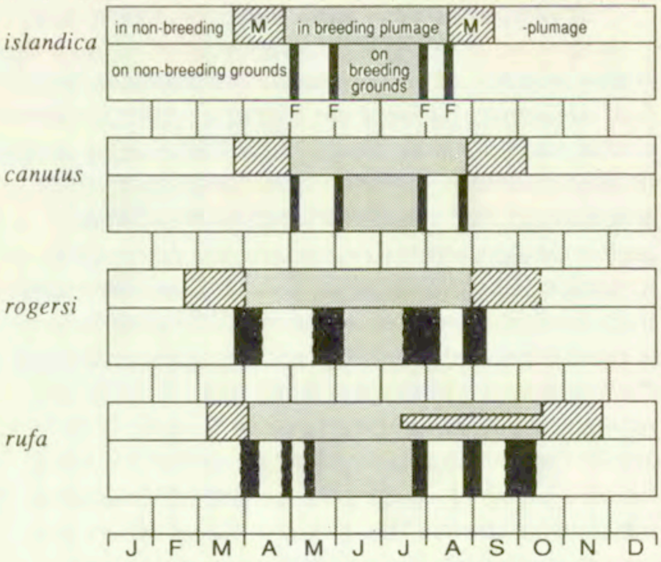

Figure 4. Tentative summary of the annual cycle characteristics in four subspecies of Knots as expressed by the timing of body moult (M) and the periods of long-distance migratory flights (F). Compiled from the information given in the review chapters in this volume and, for moult of *rogersi*, by Barter *et al.* (1988).

canutus and *islandica* Knots are remarkably similar in their seasonal timing. *Canutus* arrives slightly later on the breeding grounds and again on the wintering grounds than *islandica*, also commencing post-nuptial moult slightly later. The admittedly lesser-known trans-equatorial migrating subspecies *rogersi* and *rufa* differ from *canutus* and *islandica* by starting the moult and migration cycle earlier and finishing it later in the year (Figure 4). Since most of the breeding plumage is grown and shed on the wintering areas, *rogersi* and *rufa* carry their nuptial dress for 1.5-3 months longer than *islandica* and *canutus*, and the non-breeding plumage is carried concomitantly shorter. The trans-equatorial migrating subspecies may also have to make one or two extra long-distance flights per season, although much remains unclear about the exact itineraries of both *rogersi* and *rufa*.

Not only do the subspecies differ greatly in the distances covered per year (Table 1), but they also face very different photoperiodic regimes. To illustrate the different daylight patterns encountered as a result of migrating to a variety of latitudes, we have chosen the two best-known subspecies, *islandica* and *canutus*, and also examine the *canutus* Knots that spend the non-breeding season in southern Africa (Figure 5). *Islandica* Knots experience seasonal changes in duration of daylight which resemble those experienced by temperate latitude resident birds: increasing daylengths until midsummer and decreasing daylengths thereafter, but the pattern shows a few discontinuities when the birds migrate. The annual photoperiodic regime of those *canutus* that winter in west Africa is also 'normal', although daylengths change only marginally whilst birds are on the wintering areas. In

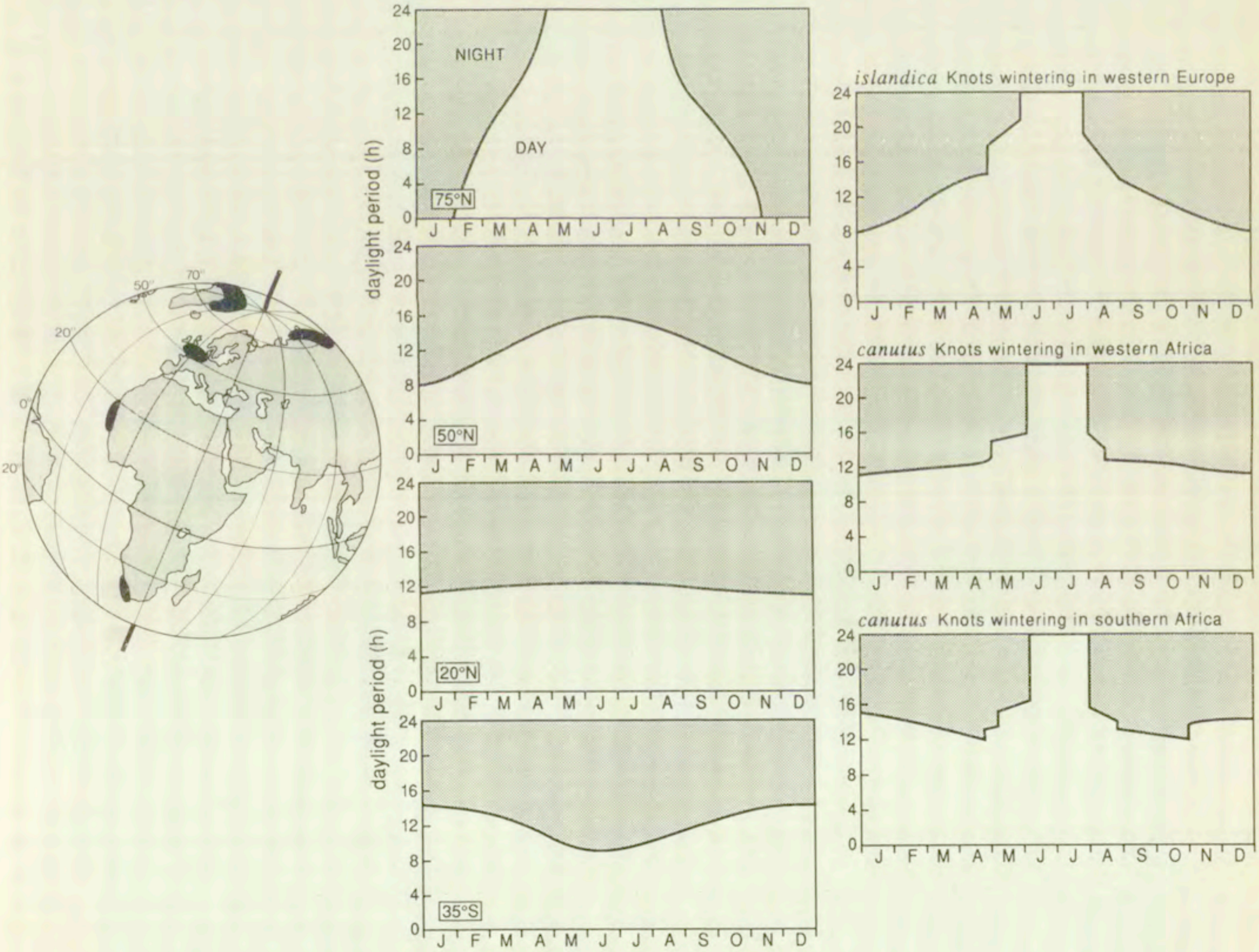

Figure 5. Summary of the seasonal changes in daylight hours at different latitudes and as experienced by three groups of Knots migrating to various latitudes. The itineraries on which the group-specific photoperiodic regimes are based, are compiled from the information available in this volume (and see Figure 6).

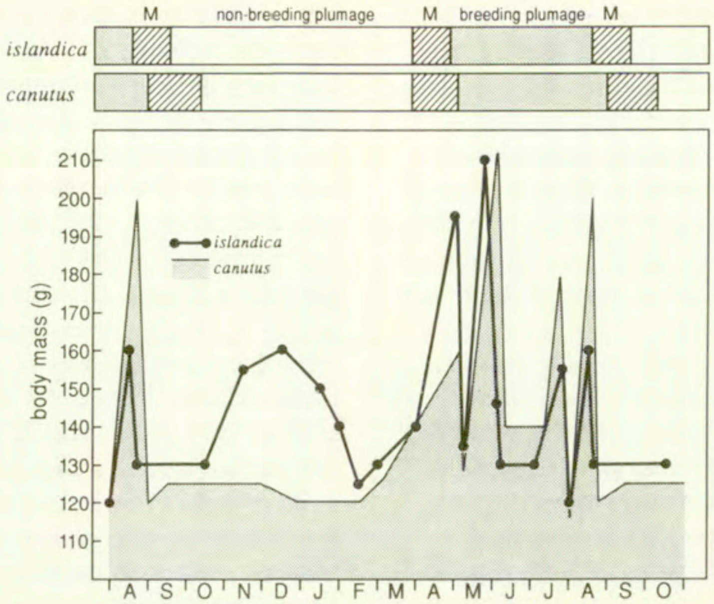

Figure 6. Tentative summary of the annual cycles in moult and body mass as experienced by the 'average' *islandica* Knot wintering in Europe and the 'average' *canutus* Knot wintering in west Africa. Compiled from Davidson & Wilson (1992), Wilson & Morrison (1992) and Piersma *et al.* (1992). The mass changes before departure from the breeding grounds in both species, and the mass changes in *canutus* before departure from Europe to west Africa, are unknown and have been surmized on the basis of minimal travel budgets and reported arrival masses.

contrast, the southern African 'wintering' *canutus* face an exotic regime, with two peaks in daylength within a year. These Knots have to prepare their migrations and breeding whilst experiencing decreasing daylengths.

Temperate non-migrant and short-distance migrants often receive their timing cues for breeding and moult from increases in daylength in spring (Murton & Westwood 1977; Wingfield & Farner 1980; Meijer 1988), but this would obviously be of little use for African wintering *canutus*. The fact that at least the trans-equatorial migrant Knots encounter unusual and erratic sequences of photoperiods make it likely that Knots organize their year with the help of an internal, endogenous, timing device, i.e. that they show endogenous circannual rhythms (Rowan 1926; Gwinner 1986a,b). Such rhythms have been found in many long-distance warbler species (Gwinner 1990), and there is firm proof that they have a genetic basis (e.g. Berthold 1990).

In the light of the daylength patterns it is interesting to take a further look at the seasonal timing of moult, fattening and migration in *islandica* and *canutus* Knots (Figure 6). *Islandica* shows the mid-winter peak in body mass commonly observed in waders wintering at northerly latitudes (Johnson 1985), but the tropically wintering *canutus* does not. The number of mass peaks in relation to migration is similar, although the mass gains achieved by *canutus* Knots before their departure from west Africa are apparently smaller than those of *islandica* before their trans-Atlantic flights from western Europe to Iceland and Norway. Overall the great similarity of the characteristics of two subspecies in spite of their large differences in migration distances and wintering latitude is striking. The only real qualitative difference is that *islandica* Knots have the typical northerly wintering mass peak which *canutus* Knots do not show. This leads us to suggest that the circannual rhythms, which are probably genetically fixed, require little modification to allow successive generations of Knots to change their migration pattern from a *canutus* to an *islandica* style. This may permit a degree of genetic continuity between at least these two subspecies.

In the light of the hypothesis about the evolutionary tree of Knots given earlier (lines of divergence from an old Siberian-breeding stock of *canutus* to the west [*islandica*] and to the east [*rogersi*, *roselaari* and *rufa*]), it is tempting to argue that the programming of the annual cycle of *canutus* (Figure 4) is flexible. If *canutus* Knots always wintered in the tropics with the current annual scheme, small changes in circannual timing (such as the timing of moult) might allow them to 'winter' even further south in (the tropical parts of) the southern hemisphere (as does *rogersi* today). At the same time (presumably small) ecophysiological adaptations may have allowed *canutus* Knots to winter at north temperate latitudes, conquer the Greenlandic and north-east Canadian arctic tundra as breeding areas (no mean achievement according to Alerstam *et al.* 1986), and thus become *islandica*.

HOT TOPICS AND UNRESOLVED ISSUES

An analysis of the evolutionary history of Knots and the possibly pivotal role of the (*canutus*?) Knots breeding in central Siberia, requires new genetic data, especially from the Siberian breeding populations. Similarly, the genetic status of Knots breeding in and migrating through Alaska requires urgent attention.

Survey work on the breeding distribution and densities of different subspecies of Knot has only just begun. The breeding of Knots in the North American Arctic needs to be mapped and the boundary, or area of overlap, between *islandica* and *rufa* checked out. Part of the breeding areas of *canutus* Knots remain to be precisely located. Breeding densities of Knots over most of the Arctic remain to be documented.

The existence, status, migration, breeding and non-breeding areas of *roselaari* Knots must be tracked down.

We know very little about the itineraries of *rufa*, *roselaari* and *rogersi* Knots, and have almost no information on the mass and body composition changes of these subspecies during their migrations. Evaluation of mass and energy losses during migratory flights in relation to the distances flown and the winds *en route* (e.g. Gudmundsson *et al.* 1991; Piersma *et al.* 1991) remains to be done properly for all subspecies.

Although some progress is being made in elucidating the resource base for the migratory performances of Knots (notably Zwarts *et al.* 1992; and Piersma *et al.* unpubl. data; Davidson in prep.), the presently available information only pertains to the *islandica* and *canutus* subspecies. The first detailed studies on the food and feeding of *rufa*, *roselaari* and *rogersi* Knots remain to be made.

Another exercise of a rather tall order is the proper documentation of the resource base in the High Arctic for breeding and migration. In fact, the ecology of the southward departure from the tundra after breeding remains one of the most understudied phenomena in the annual cycle of migrant waders.

The ecophysiological correlates of differences in 'wintering' latitude are currently under study in the *canutus* and *islandica* subspecies (Piersma *et al.* 1991). As we have seen, these two may not be too dissimilar in their annual cycle characteristics, so comparisons with latitudinal champions like *rufa* or *rogersi* hold much promise.

PROSPECT

Knots provide an intriguing example of great migratory behavioural diversity within an old species. Their small genetic diversity combined with enormous variation in 'wintering' latitude, climate and migration distance indicates the diversifying potential for small changes in endogenous circannual rhythms on migration patterns. This flexibility of a basic scheme characterizes the west African birds (*canutus*) in comparison with the European wintering subspecies (*islandica*). Since Knots offer a limited array of rather well defined stocks, which all breed in the High Arctic, they are more amenable for evolutionary studies of migration than most other bird species. We are convinced that comparative and co-operative studies of the different populations of Knots along the lines of the research programme which is presently carried out for *canutus* and *islandica*, offer great potential for interpreting the evolution of migratory pathways of waders. Indeed, we are excited about the great potential for discovery.

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