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COMMENTARY

Birds from the Far East in Central Europe: some side-notes to Pfeifer et al. (2007)

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Abstract The "reverse migration hypothesis" as the explanation for the vagrancy of Far Eastern birds in Europe is commented on. It is concluded that, as the postulated switch of 180° along a great circle line would lead the eastern or even central Siberian birds to North America rather than to Europe, the application of the "reverse migration hypothesis" to them seems untenable (which, however, does not preclude its plausibility in case of transatlantic, southern European, or even southwestern Siberian vagrants). On the other hand, patterns of appearance of the *Turdus [naumanni]* superspecies (Machalska et al. 1967) suggest the relationship of the phenomenon of vagrancy to post-breeding nomadic movements and/or periodical invasions of non-migrating species.

Keywords Invasions · Post-breeding nomadism · Reverse migration hypothesis · *T. [naumanni]* superspecies · Vagrants

Pfeifer et al. (2007) performed what they evaluate as a test of the reverse migration hypothesis supposedly explaining the occurrence of eastern Palaearctic vagrants in Central Europe. They justly observe that the overwhelming majority of papers dealing with vagrants concentrate on evaluation of particular records and only a very few discuss the causes and consequences of the phenomenon of vagrancy in general. To explain the "three general patterns": (1) "an important group of vagrants consists of eastern Palaearctic species", (2) "the relative abundance of vagrants differs considerably between species", and (3) "most recordings … occur in the autumn", two hypotheses have been proposed: the "weather hypothesis" and the "reverse migration hypothesis". Having examined the correlation between the occurrence of eastern Palaearctic species in Central Europe on the one hand, and their range size, distance to Europe, migration distance, ratio between these distances, body size, and taxonomic position on the other, Pfeifer et al. conclude that "reverse migration" is a more likely explanation of vagrancy than is the influence of weather: "errors in the migration programme (switch of the seasonal programme or reversed orientation in autumn) drive species on the great circle route from their breeding range to Central Europe".

It is not my intention to perform a comprehensive evaluation based on solid conversance with the current "state of the art" (in the last decades, my active interest has been switched from ornithology to entomology, so my orientation in recent migrational literature is deficient). Nevertheless, some—partly critical, partly supplementing—remarks seem advisable, especially in the light of facts published long ago in our (unfortunately—perhaps because of having been written in Polish, though with an English summary and diagrams which would suffice to comprehend the essence—largely overlooked) paper on Dusky Thrush *Turdus [naumanni] eunomus* (Machalska et al. 1967).

One of the astonishing results of the Pfeifer et al. study is that "the distance between the breeding range and Europe had little effects on vagrancy". This is not only strikingly counter-intuitive, but also very difficult to reconcile with their remarks on the "probability of death from starvation on the way from the breeding range to Central Europe" (evidently this probability increases with

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increasing distance) or on the dependence from migratory restlessness: "only species with a sufficiently long migratory restlessness should reach Central Europe. Otherwise, species should stop along the great circle before they reach Central Europe". If this is so, what is "sufficient" to come here from the Urals may not be sufficient for a bird from Yakoutia, and generally the closer the breeding area the greater the probability that the degree of restlessness will be sufficient! The main source of the problem seems to be the methodological convention of representing breeding (and, less importantly, wintering) ranges by their (perhaps almost or entirely irrelevant) *centers*, with no reference to the (intuitively the most likely) possibility that the majority of vagrant individuals of each particular species come from the areas closest to Central Europe. Therefore, the comparisons should be done in terms of *westernmost points* (rather than centers) of ranges. Thus, the "correlation between the number of recordings in Central Europe and the size of the distributional range" seems most conceivably interpreted as indirect, reflecting in fact the influence of the distance from the *western border* of the range, which—unlike its center—is rather strongly correlated with the range size.

Moreover, the migration distance and restlessness (and generally the genetic migration programme) are treated by Pfeifer et al. as species-specific (constant within species) features, what seems hardly acceptable even as a simplified working convention: innumerable examples of radical differences between populations, sexes, age-categories, or even individuals make any conclusion based on such an assumption highly suspect. But even so gross oversimplification does not seem to rescue the "great circle line" hypothesis as the more or less generally applicable mechanism: as clearly seen on the very picture (Fig. 1) serving Pfeifer et al. to illustrate the concept. It might perhaps "work" at most in cases of populations from *western* Siberia (or eastern Europe) migrating normally to the south-*east*, but those from central Siberia (migrating, as stated by Pfeifer et al., "to the south with little variation between species"), as a result of "switching from the autumn to the spring programme" would go across the Arctic Ocean to Greenland or Canada rather than to Central Europe. For the truly Far Eastern populations it is still worse: the *reverse* migration would bring, e.g., Dusky Thrush to Europe only if its normal wintering area is eastern or central Polynesia!

Practically all East Asiatic vagrants breed in Siberia. As far as I can recall (even if I could have overlooked some exceptional records, these could not significantly change the general rule) none of those species living to the east of Aral Sea and south of ca. 45°N has ever been reliably observed in Central Europe. This fact immediately suggests that latitudinal distribution should be taken into consideration in analysing patterns and causes of vagrancy of the species in question—and nevertheless neither Pfeifer et al., nor apparently the authors quoted by them, have paid due attention to this factor, though Pfeifer et al. seem to consider it indirectly, as represented by a secondary correlate: migration distance. This is especially astonishing in the context of a paper aiming to test the reverse migration hypothesis with its assumption of a switch of 180° along a great circle line; for that purpose, the first question one would expect to be posed is: where the birds started from and where (as exactly as possible) they arrived? And, indeed, as already remarked above, that hypothesis does not seem applicable to birds from Siberia, except for the (south-) westernmost areas. It could perhaps explain vagrancy of species living further south (Tibet, southern China), but these do not appear in Europe.

In studying the behaviour of long-distance migrants, we have the spontaneous inclination to interpret all their non-local movements as "variations on the same theme", looking for similar causes and similar mechanisms. But what if vagrancy is an entirely different phenomenon, having little or nothing to do with "classical" seasonal migrations? The two most important "discoveries" of our (Machalska et al. 1967) paper were: (1) *Turdus [naumanni] eunomus* and *T. [n.] naumanni*, occupying parapatrically the (respectively) northern and southern part of the combined breeding area, retain as vagrants in Europe essentially the same geographical relations: the former is the sole representative of the superspecies in Scandinavia, Great Britain, and along the southern coasts of Baltic and North Seas, the latter overwhelmingly dominates further south; (2) the intensity of vagrancy (both allospecies) to Europe shows a very evident (0, 1, 2, 0, 1, 3, 0, 0, 1, 5, 9, 10, 0, 0, 2, 8, 13 observations in successive decades between 1797 and 1966) ca. 50-year periodicity, with gradual increase followed by abrupt decline of the number of observed birds. This resembles the pattern of periodical invasions of non-migratory species like *Nucifraga caryocatactes* or *Loxia curvirostra*, and—it seems to me—the similarity may be more than superficial analogy! These two observations suggest two (mutually not exclusive) conceivable interpretations of the phenomenon of vagrancy:

Firstly, it is a well-known fact that in many species some (usually young) individuals nomadise after the breeding season in various directions and to various distances—this perhaps is one of the main mechanisms of territorial expansion. The movements seem rather erratic being, however, naturally restrained by the environmental conditions: the birds remain within the range of habitats similar to their "homeland". As the types of environment are—especially in northern Eurasia—more or less zonally distributed, so the long-distance nomadic wanderings must be directed predominantly to the east (it would be interesting

to know, whether European/West Siberian birds like *Phylloscopus sibilatrix* or *Erithacus rubecula* do appear as vagrants in East Siberia?) or (for Far Eastern species the only possibility) west, roughly parallel to one another. This seems the simplest explanation of more northern breeding *T. [n.] eunomus* appearing as a vagrant in northern Europe, while its more southern relative *T. [n.] naumanni* dominates further south.

Secondly, among the variables studied by Pfeifer et al., the strongest influence on ("independent contribution" to) the intensity of vagrancy had the range of distribution, in fact (admittedly) a substitute of population size, but the probable (see above) impact of the proximity of western border should also be considered! However, population size depends not only on range but also on density, and density is a highly variable feature, whose fluctuations are demonstrably or at least presumably responsible for periodical irruptions of lemmings, nutcrackers, crossbills and many other species. In my opinion, the most likely cause for cycles of vagrancy of *T. [naumanni]* in Europe is also just the periodicity of changes in population density on the breeding grounds. The factor ultimately (directly or indirectly) inducing the cyclical changes remains to be identified—among conceivable candidates are, e.g., climatic anomalies, Lotka-Volterra type of prey–predator interactions (in whichever role our thrush might appear), density-threshold dependent (e.g. epidemic) mortality, etc.—but anyway fluctuations in density of population may act as a causative factor for waves of vagrancy in at least two ways: on the one hand because, as justly expected by Pfeifer et al., "the number of vagrant individuals increases with total population size"; on the other, the increasing "pressure" (e.g. competition for food) on the breeding grounds may push even *dis*proportionally more birds out.

In both cases, it seems expectable that migratory species would also in their "nomadic" or "invasive" movements cover longer distances, and consequently appear further from their breeding grounds, than those not predisposed to long travels, which may explain the fact that all Far Eastern vagrants to Europe belong to the former group. It is also conceivable that in their westward travel the birds are, by progressive autumn cooling, increasingly "pushed" southwards, and then, at the end of the "centripetal" phase, eventually switch to the direction of their normal seasonal migration—this could be the "programme" which led some *T. [n.] eunomus* to southern parts of Europe where *T. [n.] naumanni* prevails, whereas symmetrical occurrence of the latter allospecies in northern Europe has, to my knowledge, not been observed. Unfortunately, I am aware of no other publication similarly analysing the distribution of vagrants in time and space, so I do not know to what extent other Siberian "guests" conform to the patterns found by us, but even if *Turdus [naumanni]* is an exception in showing them so clearly, the causes and mechanisms of their vagrancy should be essentially the same [Reviewer's note: Regarding the observation of latitudinal separation in both breeding and vagrancy pattern between two thrush populations it is worth mentioning that Rabøl showed a similar pattern for two *Phylloscopus* species pairs, *trochiloides/borealis* and *proregulus/inornatus*, and that the same pattern can be found in a third species pair, *fuscatus/schwarzii*.]

To conclude, I fully agree with Pfeifer et al. that "the weather hypothesis would not appear to be a satisfactory explanation for these vagrants", but the "reverse migration" favoured by them does not seem to me any more plausible! On the other hand, I am not aware of any strong evidence which would falsify the "nomadism" or "invasion" (being, perhaps, only somewhat different manifestations of essentially the same phenomenon) hypotheses—though these, of course, are for the moment only vague ideas demanding more exact elaboration and testing.

It should also be noted that the arguments set forth herein against "reverse migration" as the explanation of vagrancy concern *East Asian* birds and are not necessarily valid in case of those breeding in North America, southern Europe, or even western parts of Asia! Indeed, a glance at any map would show that for inhabitants of the eastern states of USA wintering in Middle America, for southern Europeans migrating to Africa, or for southwestern Siberian birds normally spending the cold season in southeast Asia, the end of reverse migration would be just northern or central Europe, so this seems a perfectly acceptable explanation, e.g. for *Phylloscopus orientalis* (mentioned by Pfeifer et al., though having nothing to do with Far Eastern vagrants) or, perhaps, for *westernmost populations* of *P. borealis* or *P. inornatus*. In case of transatlantic "guests", the weather hypothesis also seems quite plausible: once over the sea, land birds cannot stop off when wind becomes too strong, which they could easily do overland.

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