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Vagrancy theories: are autumn vagrants really reverse migrants?

James J. Gilroy and Alexander C. Lees

ABSTRACT Reverse migration is a popular concept, often used to explain the occurrence of autumn vagrants. The term ‘reverse migration shadow’ has been used to identify regions in which autumn vagrancy of a given species may occur, and to predict potential future vagrants to Britain. In this paper, we evaluate this theory and, by analysing vagrancy patterns, demonstrate that autumn vagrancy is not limited to the ‘shadow’ of a 180° route-reversal. Although the vast majority of individuals follow a traditional route to winter quarters, vagrancy during autumn migration occurs in all directions, and we contend that it is the pattern of observer coverage which determines the number of vagrants discovered. The occurrence patterns of some vagrants reaching Britain can be explained using the idea of long-range dispersal. We suggest that some comparatively regular vagrants reaching Britain are, in fact, performing annual migrations to presently undiscovered wintering grounds in western Europe or West Africa.

In the river valleys and on the low, densely forested hills, Leopards Panthera pardus stalk through the undergrowth, and the beautiful Asian Paradise Flycatchers Terpsiphone paradisi flit restlessly among the branches... Higher up the mountains, the bright southern birds are left behind in an enchanting sea of sounds, scents and colours. In their place stands the more solemn but equally beautiful world of the coniferous taiga, where the cool silence is perhaps broken only by the simple but sweet song of a Pallas’s Warbler Phylloscopus proregulus. (Algirdas Knystautas 1987)
alls’s Leaf Warbler *Phylloscopus proregulus* is a bird of the vast boreal forests of eastern Asia. For most European birders, however, the species is likely to conjure up images of chilly late autumn days, stunted Sycamores *Acer pseudoplatanus* and windswept headlands. To stumble upon a tiny piece of Siberia in such an abstract setting is one of the most fascinating elements of birding, not least because the discovery represents a remarkable aberration from the norm. Most people would view such a displaced individual as an unfortunate waif, the bearer of a faulty inner compass, soon to meet its destiny in the unforgiving waters of the North Atlantic.

There are many forms of vagrancy, and many theories have been constructed to explain them. For example, the frequent occurrence of vagrants in late spring can be neatly explained by the idea of overshooting: individuals migrating along the normal bearing of their original migration fail to stop within their breeding range. Others may fail to locate mates or suitable habitat on their breeding grounds and subsequently continue to an alternative destination beyond the normal breeding range. Fast-moving depressions crossing the North Atlantic are undoubtedly responsible for many Nearctic migrants from the eastern seaboard of North America reaching European coasts in autumn. The presence of a ‘blocking’ anticyclone over northwest Russia in autumn will, in some years, conspire to produce a strong easterly airflow over Europe, bringing with it a wave of disoriented migrants from Siberia or Central Asia (Elkins 1991). Even when easterly airstreams fail to develop, migrant passerines from Siberia invariably appear annually, albeit in smaller numbers. Weather systems, therefore, can be only partly responsible for carrying Asian passerines to western Europe, and the appearance of regular autumn vagrants from Siberia requires further explanation. Currently, one of the most popular theories involves the concept of ‘reverse migration’.

**Reverse migration theory**

Rabel (1969) proposed that reverse migration was a root cause of a significant proportion of autumn vagrancy, an idea later championed by Cottridge & Vinicombe (1996). The theory stems from the observation that, in order for many vagrant species to reach western Europe, individuals must re-orient at approximately 180° to their normal migration route. A logical explanation for autumn vagrancy is that these
individuals experience reversed polarity; in other words, their internal navigational mechanisms mistake north for south. By plotting species’ breeding and wintering ranges on accurate global projection maps, it is possible to extrapolate the potential ‘vagrancy shadow’ for each of these disoriented migrants.

Strong supporting evidence for reverse migration theory came from specific case studies. Cottridge & Vinicombe compared the occurrence patterns of Red-breasted Flycatcher *Ficedula parva* and Collared Flycatcher *F. albicollis* in Britain & Ireland. Both species have similar breeding distributions in the Western Palearctic, but spend the winter in quite separate regions, requiring each species to migrate in completely different directions. In autumn, most Red-breasted Flycatchers fly southeast, bound for southern Asia. Consequently, this species’ vagrancy shadow falls directly across Britain & Ireland. By contrast, the vagrancy shadow for Collared Flycatcher, which adopts a southerly heading during autumn migration to reach its wintering areas in East Africa, misses Britain entirely and shows that reversed migrants would be expected to occur in the high Arctic. The result is regular autumn vagrancy to Britain & Ireland in the former species, but not the latter. The apparent strength of this theory prompted Cottridge & Vinicombe to speculate on whether certain species might occur naturally in Britain. For example, for species such as Daurian Starling *Sturnus sturninus* and Eastern Crowned Leaf Warbler *Phylloscopus coronatus*, they suggested that natural vagrancy to Britain is ‘extremely unlikely’ because the vagrancy shadows of these species do not extend to western Europe; they would be more likely to occur in regions bordering the Bering Sea.

Problems with reverse migration theory
Along with Moss (1995) and others, we believe that the increasing use of reverse migration theory to explain autumn vagrancy in northwestern Europe may be counterproductive. In particular, the judgement of rarity records based simply upon the position of the vagrancy shadow (and taking the view that autumn vagrants occur largely in the shadow produced by a 180° reversal of migratory orientation) may prove misleading. At first glance, the occurrence patterns of most autumn vagrants from Siberia support the reverse migration model. The vast majority of such records occur in northwest Europe, as would be expected from the predominantly southeasterly orientation of Siberian breeding passerines, migrating
to wintering areas in southern China and southeast Asia. Nevertheless, this pattern also reflects the considerable bias in observer effort towards these areas (Lewington et al. 1991). At almost all other compass points to which a Siberian vagrant could orientate, observer coverage is, by comparison, negligible. Can we claim with any confidence that there are fewer vagrants moving in these other directions?

Phillips (2000) noted that vagrant Yellow-browed Warblers *P. inornatus* are not limited to landfalls along a rhumb line linking Siberia with northwest Europe. In fact, they occur at any conceivable point of the compass where there are birders to find them. This distinctive species, which is relatively easy to find, has occurred along the eastern Atlantic seaboard from Iceland to the Canary Islands, and is trapped in sufficient numbers at Scandinavian ringing stations to generate statistically significant datasets on orientation (Thorup 1998). Furthermore, Yellow-browed Warbler, along with Olive-backed Pipit *Anthus hodgsoni*, Rustic Bunting *Emberiza rustica* and Little Bunting *E. pusilla*, is a regular autumn vagrant in Israel (Shirihai 1996). In order to reach Israel, these individuals are orienting in a southerly direction, approximately 90° to their normal route, which would take them into southeast Asia. Individuals migrating in the opposite direction to their normal migration route would find themselves in the high Arctic, where observer coverage is undoubtedly too low to detect them. Nonetheless, there are occasional records there, such as a Lanceolated Warbler *Locustella lanceolata* which alighted on a vessel 110 km north of Bear Island in the Arctic Sea (Lewington et al. 1991).

Table 1. Records of vagrant Dark-throated Thrush *Turdus ruficollis* (records of subspecies *ruficollis* and *atrogularis* combined), with the approximate angle of deviation from a normal migration route, measured from the centre of the breeding range.

<table>
<thead>
<tr>
<th>Country</th>
<th>Angle of deviation from normal route</th>
<th>Number of records</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Israel</td>
<td>25°W</td>
<td>11</td>
<td>Shirihai (1996)</td>
</tr>
<tr>
<td>Egypt</td>
<td>30°W</td>
<td>2</td>
<td>Shirihai (1996)</td>
</tr>
<tr>
<td>Greece</td>
<td>45°W</td>
<td>1</td>
<td>Clement &amp; Hathway (2000)</td>
</tr>
<tr>
<td>France</td>
<td>60°W</td>
<td>11</td>
<td>Clement &amp; Hathway (2000)</td>
</tr>
<tr>
<td>Spain</td>
<td>60°W</td>
<td>1</td>
<td>Clement &amp; Hathway (2000)</td>
</tr>
<tr>
<td>Great Britain</td>
<td>70°W</td>
<td>27</td>
<td>Rogers et al. 2002</td>
</tr>
<tr>
<td>Sweden</td>
<td>80°W</td>
<td>22</td>
<td>Pulliainen &amp; Tomo (2003)</td>
</tr>
<tr>
<td>Finland</td>
<td>85°W</td>
<td>21</td>
<td>Swedish Rarities Committee (2003)</td>
</tr>
<tr>
<td>Taiwan</td>
<td>45°E</td>
<td>1</td>
<td>Clement &amp; Hathway (2000)</td>
</tr>
<tr>
<td>Japan</td>
<td>75°E</td>
<td>9</td>
<td>Clement &amp; Hathway (2000)</td>
</tr>
</tbody>
</table>

The Dark-throated Thrush *Turdus ruficollis* provides another good example of random scatter migration. This species, which comprises the nominate form ‘Red-throated Thrush’, together with ‘Black-throated Thrush’ *T. r. atrogularis*, breeds from western and central Siberia, east through western Mongolia to northwestern China. Its winter range lies to the south of the breeding range, extending from Iran and Kazakhstan through the Indian subcontinent to the Tibetan Plateau, northern Myanmar to northeastern China. Vagrants have moved in most directions around this route (table 1). In this case, birds arriving in Britain cannot be reverse migrants, as the reverse migration shadow of Dark-throated Thrush falls over the Russian Arctic. Many other regular autumn vagrants reaching western Europe also have reverse migration shadows which completely miss Britain & Ireland, yet still occur here. Examples include Black-winged Pratincole *Glareola nordmanni*, Pied Wheatear *Oenanthe pleschanka*, River Warbler *Locustella fluviatilis*, Eastern Olivaceous Warbler *Hippolais pallida* and Isabelline Shrike *Lanius isabellinus*.

Turning to regions beyond Europe, one area with a high concentration of birders is North America. Here the vagrancy patterns are strikingly different. In California, the annual appearance of vagrants from the eastern seaboard is celebrated in a similar fashion to the arrival of Siberian vagrants in Europe. In this case, species which normally migrate along the eastern seaboard to the Caribbean and beyond must
migrate in a direction ranging between 45º and 90º to the west, carrying them across the North American landmass, to make landfall on the west coast. Among the most frequently recorded vagrant passerines reaching California are Blackpoll Warbler Dendroica striata and Baltimore Oriole Icterus galbula, and their occurrence is seemingly unrelated to weather patterns (Patten & Marantz 1996). In addition, many Palearctic breeding passerines now turn up in California. Of these, Red-throated Pipit Anthus cervinus is regular, while Dusky Warbler Phylloscopus fuscatus, Olive-backed Pipit and Rustic Bunting have all been recorded.

The charismatic and easily recognisable Scissor-tailed Flycatcher Tyrannus forficata provides an interesting example. It breeds in the southern prairie region of central North America, as far north as Kansas, and follows a precise route on autumn migration, along the Gulf of Mexico to winter in the southern Caribbean. Reverse migration along a 180º line would place the vagrancy shadow in central Canada, east of the Rockies. In this case, however, birder coverage is good in all directions around the breeding range and, consequently, there are records in almost every North American state. Vagrants have reached the west coast, north almost to Alaska, and have occurred throughout the eastern seaboard states north to Nova Scotia (Sibley 2000).

It is evident that vagrant birds can travel in all directions, including a bearing opposite to the normal direction of migration (Alerstam 1990; Lewington et al. 1991), and we contend that apparent peaks in occurrence in reverse migration shadows often correspond with areas of high observer coverage. Interestingly, the term ‘reverse migration’ has another use in defining an unrelated migratory phenomenon. Experiments devised to measure the migratory orientation of birds have shown that a proportion of migrants at a stopover site will often orient in the opposite direction to the majority (Wiedner et al. 1992; Akesson et al. 1996). To demonstrate this, Akesson et al. (2001) conducted a radio-tracking experiment using Reed Warblers Acrocephalus scirpaceus which exhibited reversed migration orientation at Falsterbo, Sweden. These individuals moved in the opposite direction to that of normal migration for up to two days before reversing their orientation again and resuming their normal migration direction. This phenomenon has been explained as a short-term motivational conflict, experienced by migrants reaching an environmental boundary or obstacle (Karlsson et al. 1996). A typical example would be a sea crossing (as in the Falsterbo experiment): some weaker individuals may decide not to attempt to cross, and instead backtrack along their previous heading, to refuel at a known feeding site, before making another attempt (Akesson et al. 1996; Akesson 1999). This short-term phenomenon is, however, unlikely to be a cause of regular vagrancy.

The main function of a vagrancy theory is to make sense of our observations and records.

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286. Pallas’s Leaf Warbler Phylloscopus proregulus, Voe, Shetland, October 1982. The chill of late autumn, Sycamores Acer pseudoplatanus, and windswept and remote places: classic conditions for an autumn Pallas’s Leaf Warbler. And this is often a fairly typical view of this species in Britain, high up among the blowing Sycamore leaves, in and out of view, forever on the move.
Reverse migration theory is useful in that it offers an explanation for differences in the frequency with which various species are recorded. Without this framework, we are left with little to account for the surprising abundance of some species, and the absence of others. In the remainder of this paper, we will examine a number of alternative concepts, and attempt to provide an explanation for some of these patterns, by looking at vagrancy as a form of dispersal.

**Vagrancy and dispersal**

Migration is a complex process, and birds use many different cues as navigation aids, including visual, olfactory and magnetic stimuli (Wallraff 1996, 2001; Walinder et al. 2001). An inability to use any one of those cues could result in a bird migrating in the wrong direction. One potential cause of vagrancy is genetic mutation. Evidence suggests that migratory instincts, including orientation, are coded precisely in a bird’s inherited genetic configuration (Freeman & Herron 2001). If this was not the case, how else could, for example, a juvenile Common Cuckoo *Cuculus canorus* perform its migration to Africa unaided? Given this strong genetic basis, it is clear that simple mutations could affect any of the behaviours involved with migration. It is, therefore, inevitable that some individuals will be born with migratory instincts which differ from those of the rest of the population.

The difficulty with this ‘simple mutation’ explanation for vagrancy is the frequency with which certain vagrants occur. Such mutations are almost certainly too rare to be responsible for the relatively large numbers of Richard’s Pipits *Anthus novaeseelandiae*, Yellow-browed and Pallas’s Leaf Warblers which occur in northern Europe each year. No known species has such a high rate of novel phenotypic mutation (Freeman & Herron 2001). Normally, this discrepancy would be accounted for by reverse migration theory, or by invoking non-genetic causes of vagrancy. Navigation is a difficult business, and perhaps some young individuals, though genetically endowed with the means to navigate correctly, can still make errors through inexperience. Weather, of course, will always play a part in determining the numbers of vagrants arriving (Moss 1995).

Another hypothetical explanation builds on the idea that autumn vagrants act as agents of dispersal by colonising new wintering areas (Williamson 1975; Alerstam 1990; Sutherland 1998). Imagine the following scenario. The world population of a certain abundant migra-
tory species migrates each year from breeding grounds in Siberia to winter quarters in southern India. Successive generations inherit the orientation of this migration genetically, such that juveniles can perform the entire migration in isolation from other birds. Occasionally, mutations occur in this population, with juveniles dispersing in random directions away from their normal route. One year, a small number of these mutant juveniles locate suitable wintering habitats in the Mediterranean region, and survive. After retracing their migration route to Siberia the following spring, they breed, and the mutant orientation genes are passed to some of their offspring. If these offspring follow a similar orientation and are able to locate and survive in the new wintering habitat, this new orientation could proliferate in future generations. In this way, vagrants are able to expand into suitable but previously unoccupied wintering areas and exploit vacant niches that may benefit the species’ survival in the long term.

How likely is this scenario? Helbig (1991) conducted a series of laboratory experiments in which individuals from two subpopulations of Blackcaps Sylvia atricapilla were interbred. Each subpopulation uses an entirely different migratory route in autumn: birds from central Europe move southwest, while those from eastern Europe migrate southeast (Berthold 1988). The migratory orientation of hybrid offspring was found to be intermediate between those of the two parents. Other experiments have produced similar findings (e.g. Helbig 1996, Pulido et al. 2001). This evidence suggests that, in order for a new migratory orientation to be passed from generation to generation, both parents would have to share the same abnormal orientation genes. Genes are complex entities, however, and in some cases only one parent would need to carry the mutant gene in order for some of the offspring to show the abnormal characteristic, as a result of an allelic dominance relationship (Freeman & Herron 2001). Of course, if the entire migratory orientation was learned from the parents, as it is in some species, rather than inherited, the likelihood of offspring finding the new winter site would be significantly higher (Baker 1980; Sutherland 1998). It is possible that just such a development may now be occurring in the case of Pine Bunting Emberiza leucocephalos. This Siberian breeding species winters primarily in Asia, from the central Himalayas to northeastern China, and until recently was only known as a vagrant to the Western Palearctic. Small populations have been discovered wintering in Israel (Shirihai 1996), and more recently in western Italy (Occhiato 2003). As these birds, including adults and first-winters, return annually to specific and localised regions within each country, it appears that small but stable migratory subpopulations, perhaps with a genetic abnormality affecting their navigational abilities, have become established outside the normal wintering range.

Previous authors, including Williamson (1975), Cottridge & Vinicombe (1996) and Sutherland (1998) have alluded to the possibility that a small number of vagrants could stumble upon successful wintering areas by chance. The frequency with which some regular ‘vagrants’ occur in Britain could, therefore, be explained by these birds being part of a surviving population, established by ‘genuine’ vagrants at some time in the past. Such birds may now be wintering at low densities somewhere in southern or western Europe or West Africa, and returning to the breeding grounds to mate with birds sharing a similar genetic abnormality, to produce offspring with the same migratory orientation. Not so long ago, birdwatchers in Britain considered Pallas’s Leaf Warbler to be one of the rarest vagrants reaching these islands, with only three records prior to 1958 (Cottridge and Vinicombe 1996). Today, Pallas’s Leaf Warbler occurs annually in Britain, with numbers exceeding 100 individuals in some years. It is theoretically possible that this species has recently established a new winter range, and is using Europe as a migratory flyway. Although we think of them as vagrants, they may actually represent a biologically significant population, following a genuine annual migration.

This hypothetical scenario might be referred to as ‘pseudo-vagrancy’. Table 2 lists several species from northern European and Asian breeding ranges which normally winter in southern and southeast Asia. European records of all of these species have increased in the last 50 years. We contend that these patterns could be explained if these birds were, in fact, ‘pseudo-vagrants’, performing annual migrations to presently undiscovered wintering grounds.
British vagrants as ‘legitimate’ migrants?

Does our knowledge of European vagrancy patterns support the ‘pseudo-vagrant’ theory? A hypothetical Siberian ‘pseudo-vagrant’ wintering in southern Europe or western Africa would logically follow the most direct route, taking it over the Eurasian continental landmass. Its detection is possible only when it is forced to make landfall: after drifting to the British or Scandinavian coastline in autumnal easterly winds, for example. In most winters, a handful of Siberian passerines attempt to overwinter in Britain & Ireland; the winter of 2002/03 produced wintering records of three Yellow-browed Warblers, two Richard’s Pipits, plus Dusky Warbler, Little Bunting and Blyth’s Pipit Anthus hodgsoni (Birding World 15: 312-318, 2002). These numbers are, however, a fraction of those found in autumn, perhaps suggesting that conditions here may not be suitable for the long-term survival of such birds en masse.

Farther south, however, the story is rather different. Richard’s Pipits winter regularly in France, Spain, Portugal and Morocco, and return annually to the same well-watched sites. Sizeable flocks have included up to 18 together in Spain (de Juana et al. 2000), 15 in Morocco (Brit. Birds 92: 64-82) and four in France (Brit. Birds 92: 278-300). Yellow-browed Warblers are also wintering in Iberia in increasing numbers (Brit. Birds 85: 6-16). Could such winter records be representative of a much more widespread pattern, involving other species? Observer coverage may hold the key to this question. Consider the parallel phenomenon of the so-called ‘Shetland specialities’. Certain species, including Lanceolated Warbler and Pechora Pipit Anthus gustavi, occur regularly in the Northern Isles, but only rarely elsewhere in Britain. Perhaps some of these species do occur in larger numbers away from Shetland, but go unnoticed elsewhere in Britain & Ireland, as their skulking nature precludes detection in all but the bleakest of habitats. One might argue that the paucity of wintering ‘pseudo-vagrant’ records could be similarly explained. Once birds such as Yellow-browed Warblers have moved away from coastal migrant traps and dispersed inland to woodland, scrub and farmland habitats, their detection rate will surely drop dramatically, even in areas where there are plenty of birders. If these ‘pseudo-vagrants’ have the capacity to reach North Africa, their detection would be near impossible, yet small numbers of vagrants originating from Siberia have been recorded there (Bergier & Bergier 1989), suggesting that the true numbers involved could be much higher.

The paucity of records of these species in western Europe in winter and spring does, however, present a major stumbling block for the theory. Even if these hypothetical ‘pseudo-vagrants’ go unnoticed on their wintering grounds, surely some would be located again in the spring, as they pass through areas with a high concentration of observers? For most species, however, spring migration routes are different to routes used in autumn. In general, spring migrants also adopt a greater urgency, with birds migrating faster, and making fewer stopovers, than in autumn (Moss 1995). In autumn, inexperienced first-year birds, lacking

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**Table 2. Examples of possible Siberian ‘pseudo-vagrants’, i.e. species passing through Europe in small numbers on migration to newly colonised wintering areas. The species listed at the head of the table are those recorded most regularly in Britain, and hence are considered to be the most likely ‘pseudo-vagrants’, with the likelihood reducing towards the foot of the table.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Likelihood of being a ‘pseudo-vagrant’</th>
</tr>
</thead>
<tbody>
<tr>
<td>Richard’s Pipit Anthus novaeseelandiae</td>
<td>Higher</td>
</tr>
<tr>
<td>Yellow-browed Warbler Phylloscopus inornatus</td>
<td></td>
</tr>
<tr>
<td>Red-breasted Flycatcher Ficedula parva</td>
<td></td>
</tr>
<tr>
<td>Pallas’s Leaf Warbler Phylloscopus proregulus</td>
<td></td>
</tr>
<tr>
<td>Little Bunting Emberiza pusilla</td>
<td></td>
</tr>
<tr>
<td>Rustic Bunting Emberiza rustica</td>
<td></td>
</tr>
<tr>
<td>Dusky Warbler Phylloscopus fuscatus</td>
<td></td>
</tr>
<tr>
<td>Radde’s Warbler Phylloscopus schwarzi</td>
<td></td>
</tr>
<tr>
<td>Olive-backed Pipit Anthus hodgsoni</td>
<td>Lower</td>
</tr>
<tr>
<td>Lanceolated Warbler Locustella lanceolata</td>
<td></td>
</tr>
<tr>
<td>Yellow-breasted Bunting Emberiza aureola</td>
<td></td>
</tr>
<tr>
<td>Pechora Pipit Anthus gustavi</td>
<td></td>
</tr>
</tbody>
</table>
a similar urgency to reach their wintering grounds, are more likely to make prolonged stopovers. Following the winter, during which these more experienced and capable survivors have had time to lay down fat reserves prior to migration, the return journey to the breeding areas occurs rapidly, and with only the minimum number of stopovers, often during periods of inclement weather.

The Aquatic Warbler *Acrocephalus paludicola* is one example of a possible 'pseudo-vagrant'. With its breeding range centred on Belarus, and extending to the German-Poland border, Lithuania, Hungary, Ukraine and western Russia, occasional autumn records in Britain were formerly treated as vagrants. Since the early 1970s, intensive ringing studies in coastal reedbeds throughout southern England have
revealed a small but regular autumn passage through this region (Gorman 2002; Wernham et al. 2002), and it now seems that the entire world population of Aquatic Warblers migrates along a precise route through a staging area in western France and Belgium, with southern England receiving a small proportion of the total numbers involved. But, despite this now well-known passage through western Europe, the exact wintering range of Aquatic Warbler still remains largely unknown. There are just a handful of winter records from Senegal, Mauritania, Mali and Ghana (Cramp 1992; Wernham et al. 2002), and it seems that the entire population of a European breeding species is able to elude detection for several months of the year. The paucity of spring records from western and central Europe is also striking, although in recent years, increased ringing effort in Spain has revealed the existence of a small spring passage there (A. van den Berg, verbally). Here we have a species which maintains a viable population, migrates through western Europe to winter in West Africa, and yet is rarely seen in winter or spring. Parallels can be drawn between this species and any regular autumn vagrant. It is true that Aquatic Warblers are inveterate skulkers, and difficult to find without a mistnet, yet their specific habitat requirements might make them easier to locate on their wintering grounds than more generalist species. If wintering populations of ‘pseudo-vagrant’ species are small and widely dispersed, the detection of even a few individuals could be seen as being indicative of a much larger overall population.

In recent years, Blackcaps have overwintered in Britain in increasing numbers. Ringing recoveries have shown that most of these originate in eastern Europe (Berthold 1988; Berthold & Helbig 1992). In order to reach Britain from their breeding grounds, these individuals migrate northwest: a 90° aberration from their normal Mediterranean-bound route. Evidently, this population was established after individuals with ‘faulty’ migratory orientations were able to overwinter successfully in Britain, and return to breed with birds sharing a similar directional and migratory abnormality. Apparently, the arrangement is advantageous, as the number of Blackcaps wintering in Britain is on the increase (Berthold 1988). This example is undoubtedly representative of a more general frequently occurring pattern amongst migratory species.
The disjunct wintering ranges of species such as Sociable Lapwing *Vanellus gregarius* and Red-throated Pipit, which winter in both southern Asia and East Africa, or the increasing numbers of migratory hummingbirds from the western United States wintering at garden feeders in the eastern USA (Calder 1995) may be further examples. A review of migratory plasticity by Sutherland (1998) described 43 similar cases in which species have significantly changed their migration routes in historical times. Could the ‘pseudo-vagrants’ listed in table 2 be further examples of this phenomenon?

**Conclusions**

Our aims in writing this paper were twofold. First, we wished to raise some questions about the reverse migration theory and, in particular, to highlight the dangers of using it to predict which species might occur as vagrants in western Europe. Reverse migration is a genuine short-term condition, potentially affecting any migrant faced by a large barrier to passage. The use of ‘reverse migration theory’ in order to establish the vagrancy potential is, however, likely to be counterproductive when determining the likelihood of vagrants reaching western Europe. We suggest that true autumn vagrancy occurs primarily as the result of inherited genetic abnormalities which affect the navigation systems of an unknown proportion of the population of most migratory species. Such individuals may migrate in any direction, not only in the reverse direction. This variation may also lead to individuals migrating abnormally long distances and, in extreme cases, remarkable extralimital records.

Second, we wished to discuss a different framework for understanding the vagrancy phenomenon: as a form of dispersal. The idea that vagrants can establish new wintering populations is not new but, we feel, deserves greater attention, not least for the potential conservation implications in today’s changing landscape. It is anticipated that the ‘pseudo-vagrant theory’ proposed here will at least provide a basis for further discussion on how the relative frequency with which certain species appear in
Britain may be explained. At present, the collective understanding of winter bird distributions is insufficient either to prove or disprove the theory. Only through increasing observer coverage and awareness, particularly in presently under-watched regions, will we add some much-needed clarity to this debate.

Acknowledgments

We would like to thank P. Kennerley, D. Smith, D. Gilroy and two anonymous referees for comments on the manuscript. Thanks also go to S. Mahood and R. Addison for their help in conceptualising this paper.

References


