MIGRATORY BEHAVIOUR OF BLACKCAPS (*SYLVIA ATRICAPILLA*) WINTERING IN BRITAIN AND IRELAND: CONTRADICTORY HYPOTHESES

Przemysław Busse

ABSTRACT

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There was observed clearly pronounced growth of population of Blackcaps wintering in Britain and Ireland. These winterers are of continental origin. The problem is in causes of the phenomenon - firstly the migratory behaviour involved and secondly, mechanisms leading to positive selection of individuals belonging to the group migrating from central Europe to the British Isles. Migratory behaviour model, called here "direction shift model", proposed by Berthold and Terrill (1988) is discussed and alternative "reverse migration model" is proposed. The latter assumed that most of the autumn continental immigrants to the British Isles reach them by reverse track of normal migration directed to three winter-quarters. After arrival they reorient migration to backward track or, if they are interpopulational hybrids, change direction according to other inherited navigation programme. Minority of immigrants already is at reoriented track, after reorientation at Norwegian coast. British winterers originate from both simple reverse migrants, but mainly from a stock of reoriented birds. The model is built on reanalysis of accessible ringing data and confirmed by the results of winter counts of wintering Blackcaps and the data from field navigation experiments reported elsewhere.

P. Busse, Bird Migration Research Station, University of Gdańsk, Przebendowo, 84-210 Choczewo, Poland.

INTRODUCTION

The migratory behaviour of the Blackcap was discussed, or at least mentioned, in many papers. One of the reasons is that this species shows clearly visible "migratory divide" caused by migration of west and east European Blackcaps in very different directions: SW and SE respectively. The birds inhabiting central Europe show apparently not clear, "fan-shaped" pattern of migration. The reasons of the phenomenon were explained differently and they will be discussed later. In recent years the Blackcap has focused attention of ornithologists as there was observed a rapid growth of a number of Blackcaps wintering in Britain and Ireland (Langslow 1979, Leach 1981, Bland 1986), where wintering individuals of this species were in the past recorded sporadically (Witherby 1938, Stafford 1956, Williamson and Whitehead 1963, Rice 1970, Leach 1981, Simms 1985). This unique phenomenon of creating a new winter-quarter of the species caused publication of a paper by Berthold and Terrill (1988) discussing origin of the new migratory pattern and the reasons of rapid growth of the population involved. According to a feeling of the authors, expressed in the last sentence of the paper, that this population offers a genuine challenge for complex studies, I will re-analyse accessible data on migratory behaviour of Blackcap, because presented in the paper fundamental hypothesis on the origin of the behaviour seems to be an unacceptable one.

HYPOTHESIS INQUIRED: "DIRECTION SHIFT" MODEL OF BLACKCAP MIGRATION

Berthold and Terrill *(op. cit.)* formulated the hypothesis as follows (Fig. number changed): "Rice (1970) has already pointed out that possible explanations for the origin of the migratory behaviour need not evoke major changes in existing patterns. Many central European Blackcaps migrate, in autumn, in a southwesterly direction (Zink 1973). The angle of normal migration need only be rotated northwest by about 30 degrees for continental Blackcaps to reach Britain

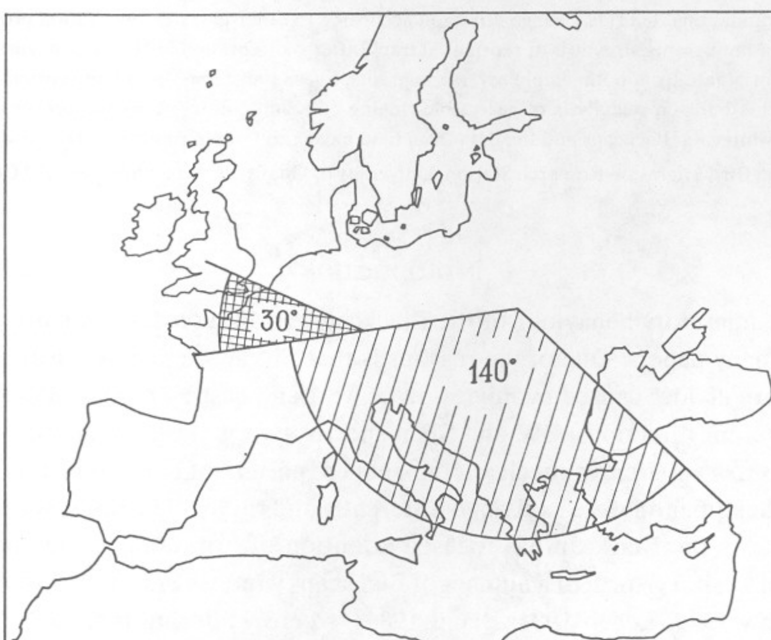


Fig. 1. "'Fan-shaped' pattern of all migratory direction taken by Blackcaps breeding in Europe (after Zink 1973). Note that the angle of 'normal' migration need only be increased by about 30 degrees for these birds to reach Britain and Ireland." (after Berthold and Terrill 1988).

in autumn (Fig. 1). Currently, we know relatively little of the genetics of migratory behaviour, but the "fan-shaped" pattern of migration of Continental Blackcaps suggests a continuous distribution of behaviour with respect to direction (Fig. 1). Essentially we are proposing that one of the tail ends of a continuous distribution of a behavioural trait (westerly component in orientation during autumn migration) that was previously selected against is now strongly selected for. (...) we feel that the above explanation is the most parsimonious and is therefore an appropriate starting place for the scientific inquiry".

DOUBTS AS TO THE HYPOTHESIS

Discussing the hypothesis, the authors wrote that from the extensive amount of research already performed on Blackcaps it is known that "the distance and duration of autumn migration (and probably direction as well - see Berthold 1984) are highly fixed behavioural traits". Then they skiped the basic problem of the change in direction of migration by calling it "a slight increase in the westerly component of autumn migration" and they concentrated on the time-distance programme of migrants (inherited too). So, they have taken the view clearly contradictory with the position of Berthold in the mentioned paper: "Hence typical migrants appear to a large extent as endogenously-controlled 'automates', equipped with inherited programmes for the necessary spatial, temporal and ecological orientation during their migration". The navigation "automates", which can lose direction by 30 degrees from a maximal inherited deviation are really not able to effective navigation. This hypothesis is therefore in clear contradiction with real navigation abilities observed in Blackcaps migrating to African winter-quarters. Hitting these limited areas is possible only when dispensable navigation error is at a level of few degrees. The next doubts as to the hypothesis discussed are as follows:

1. The authors overlooked the fact that north-western France is empty of recoveries of birds originating from central Europe, so the birds which reach Britain must skip 30 degrees instead of continuously widening one tail end of migration pattern,

2. Although the authors based on Zink's (1973) data, they took into consideration only few recoveries with the smallest "deviation", while on the same map there are recoveries with further deviation to N by up to the next about 90 degrees. The problem will be discussed later.

MIGRATION PATTERN OF EUROPEAN BLACKCAPS

Any discussion of special migratory behaviour of the birds must take into consideration general migration pattern of the species. Recoveries of individuals ringed as nestlings or breeding birds, are basic data for presenting the pattern while those caught at migration help to solve special problems.

The patterns of migration of Blackcaps originating from three areas are shown at Figure 2. British birds migrate mainly in direction of Spain and Gibraltar, much less frequently more to the East as far as Sardinia and Corsica. Scandinavian Blackcaps mainly, migrate SE through Cyprus and Middle East mainly, with singletons directed to Italy and Scotland. Central European birds migrate in direction of both earlier mentioned areas but to Italy too. A classic method of mapping ringing recoveries, as adopted at the Figure 2 to British and Scandinavian birds, show here very characteristic, "fan- shaped" or wide-angle

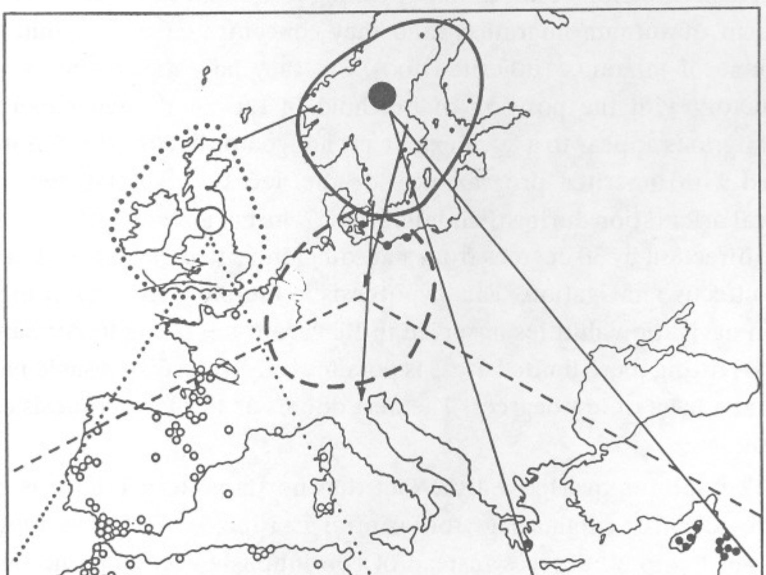


Fig. 2. Migration pattern of European Blackcaps based on recoveries of birds ringed as pulli and breeding individuals. Two areas of narrow angle of migration (recovery places and, in Scandinavia, ringing localities are shown; arrows represent exceptional recoveries) and one area of wide-angle ("fan-shaped") migration (after data of Zink 1973).

migration pattern (detailed map is published elsewhere - Busse 1986a, 1987a). First interpretations of this pattern (Brickenstein-Stockhammer and Drost 1956, Williamson and Whitehead 1963, Williamson 1964) stressed migratory divide pattern and localised divide zone at 11 degrees E (Williamson and Whitehead 1963) or 15 degrees E (Klein *et al.* 1973). The latter authors stated that the divide occurs below 52 degrees N only and is caused by proximity of the Alps. Generally, conception of migratory divide bases on the assumption that all directions from ringing to recovery places should be classified dichotomically to SW or SE directions of migration. Then most of Italian recoveries was classified as belonging to SW migrants. This dichotomy was called in question by Busse (1986a), who divided recoveries of Central European Blackcaps onto three (instead of two) groups - these migrating to/through Iberian Peninsula, Italy and Balcan Peninsula. The Blackcap migration pattern was shown as an example of a new explanation to wide-angle (or "fan-shaped") migration patterns occurring in a number of Central European birds. The hypothesis is that the area inhabitants of which show wide-angle migration pattern is a mixed zone between different

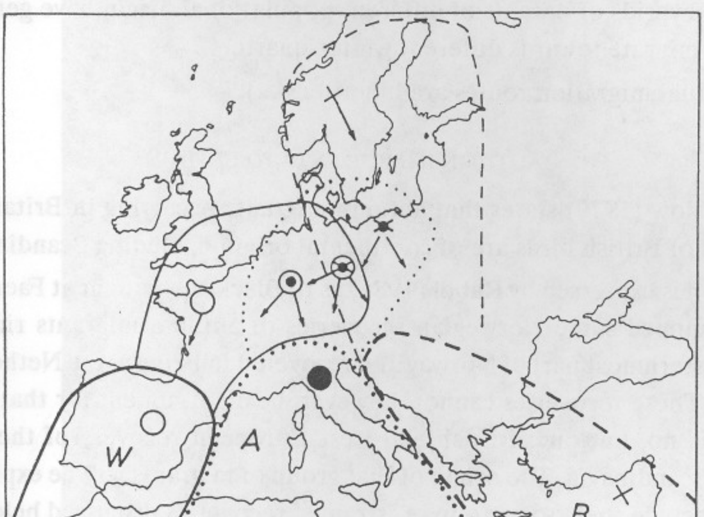


Fig. 3. Population pattern of European Blackcaps (after Busse 1986a). Breeding areas of birds directing migration to three winter-quarters (W - "western", A - "Apenine", B - "Balkan") are delimited. Mixed zones are pointed by combined signs.

populations. Re-analysed from this point of view recoveries of European Blackcaps have shown populational pattern presented at Figure 3 (for details see *op. cit.*). A theoretical model for the accepted interpretation of the pattern is discussed in the paper by Busse (1986b) and presented in an extended summary of the lecture (Busse 1987b) given at The Euring Technical Conference in Wageningen. A few of the basic assumptions of the model should be listed here, as they play an important role in the further discussion of migratory behaviour of the Blackcap:

1. The wintering area of European migrants can be divided into separate winter-quarters localised at late ice-period refuges of the species (...); for long-distance migrants these areas are the first parts of Europe occupied in the past by the populations invading the continent from the south - this determines the actual pattern of migration.

2. Winter-quarters are occupied at winter-time by a defined population, members of which are genetic descendants of birds which started their dispersion from this area to central and northern Europe in the period after the ice age.

3. Wintering at defined winter-quarters is genetically coded; individuals which are hybrids of parents of different populational origin have genetic possibilities to migrate towards different winter-quarters.

4. Actual migration routes are inherited (...).

AUTUMN IMMIGRANTS TO BRITAIN

Langslow (1979) states that autumn migrants occurring in Britain after the departure of British birds are of continental origin, including Scandinavia. Similar opinion is expressed by Rabøl (1985) as to Blackcaps caught at Faeroe Islands. He has mapped some Norwegian recoveries of autumn migrants ringed at the south- westernmost part of Norway and recovered in Britain, the Netherlands and Belgium. These recoveries cannot, however, be an argument for that statement, as there is no, but one, British and west European recovery of the Blackcaps native in Scandinavia. The origin of that group of migrants will be explained later as I will include them to a group of "strange" recoveries discussed below.

"STRANGE" RINGING RECOVERIES OF BLACKCAPS

As it was stressed earlier, the "normal" directions of Blackcap autumn migration are SW to SE. Studying Zink's (1973) atlas of ringing recoveries of Blackcap one can find dozen or so recoveries which do not fit this simple rule. These recoveries were so distinct, that most of them was localised on a special map and called autumn birds migrating in false directions. Number of the similar further recoveries was added by Langslow (1979) and Schlenker (1981). They can be found too in 1987 report on bird ringing in Britain and Ireland (Mead and Clark 1988). Blackcaps migrating in "atypical" directions were found in the Baltic area too. Out of 33 Blackcaps recoveries of birds ringed during Operation Baltic work as much as five travelled in strange directions (WSW, W, WNW, and two NW!), which clearly cannot be accepted as normal in that part of Europe. Basing on Zink's (1973) and Polish data I calculated that as much as about 7.5% of Blackcaps ringed at autumn migration show then "strange" direction of further passage. This is an extraordinary high proportion and it seems to be unique, as to frequence phenomenon in European Passerines, e.g. out of few hundred recoveries of Robins (*Erithacus rubecula*) ringed by Operation Baltic only one or two show "wrong" direction of autumn migration.

Altogether 44 Blackcap recoveries derived from mentioned sources show clearly "false" direction of migration and next 22 recoveries are atypical as to destination or origin (Rabøl 1985 and Operation Baltic data).

MIGRATION PATTERN OF THE "STRANGERS"

The "strangers" may be grouped into clusters. Some of them are presented at Figures 4-6. The groups are quite clearly differentiated as to directions of the movement - these are opposite to normal migration routes towards areas shown at Figure 3, which is a basic assumption of the hypothesis explained below; the strange recoveries mapped there can be treated as documents of reverse migration in sense of what Evans (1968) and Rabøl (1976, 1978, 1985) stated. The birds mapped at Figure 4 show the reverse pattern of migration, which should normally lead migrants to Middle East through Balkan Peninsula. It is very characteristic and important that tracks of Baltic reversed migrants are different from strictly central European but they lead to the same goal. All these tracks cover the easternmost tail of "fan-shaped" migratory pattern of central European Blackcaps. The other group of strangers (Fig. 5) clearly contains reversed "Italians", while the next one (Fig. 6) - the birds with inherited, but reversely read SW orientation programme. At the last Figure there are mapped three recoveries of the birds, which showed "normal" SW direction of the movement. One can ask, why they are treated as the strangers, but

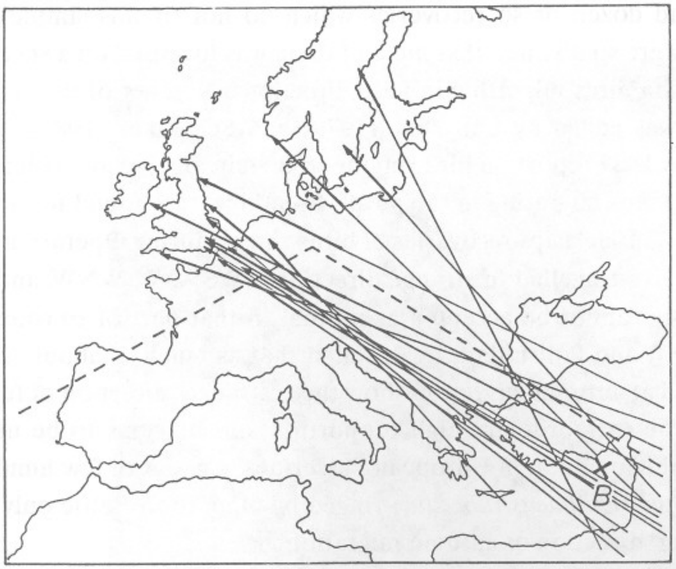


Fig. 4. "Strange" recoveries of Blackcaps - reverse B winter-quarter migration. Arrows connect ringing and recovery places.

fig.5

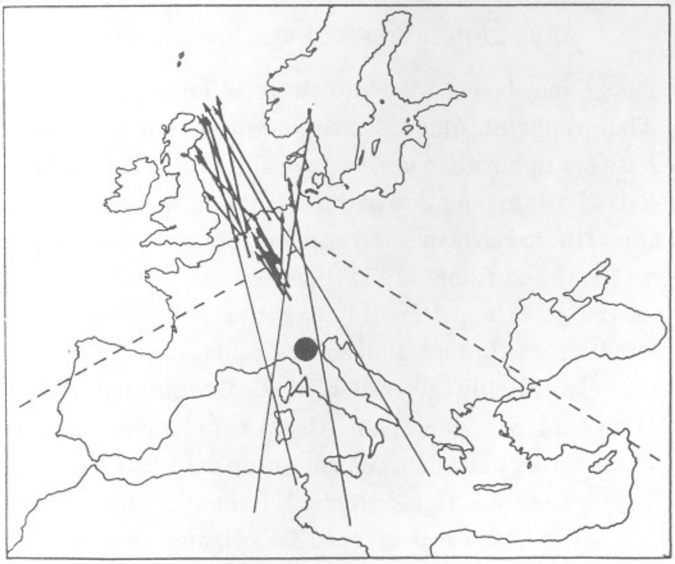


Fig. 5. "Strange" recoveries of Blackcaps - reverse A winter-quarter migration. Arrows mean the same as at Figure 4.

fig.6

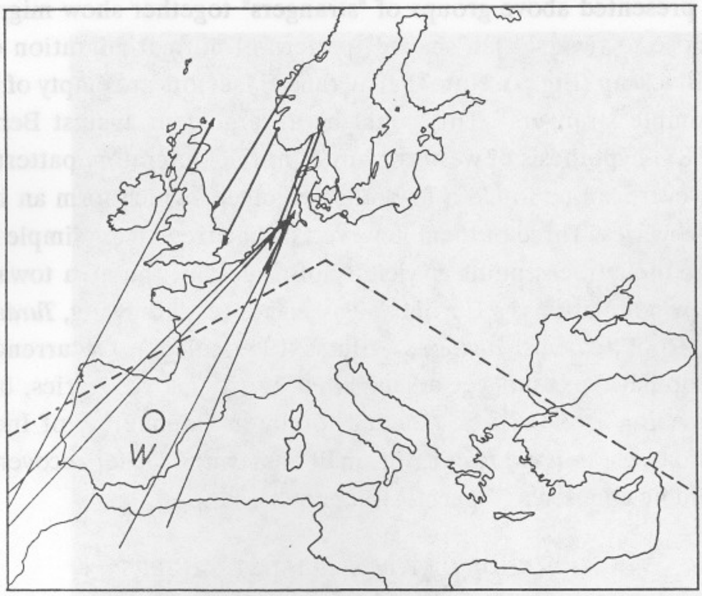


Fig. 6. "Strange" recoveries of Blackcaps - reverse W and back reoriented W winter-quarter migration. Arrows mean the same as at Figure 4.

after a glimpse at Figure 2 the answer is that no Blackcap originating from Norway migrate SW. Therefore these three recoveries must be treated as coming from the birds, which first travelled by reverse migration track, then reoriented themselves at Norwegian coast (they were ringed there) and returned, navigating according to unaltered orientation programme leading to "W" winter- quarter on Iberian Peninsula. Possibility of such re- orientation is documented by Rabol (1985). Figure 7 shows some more examples of re-oriented reverse migrants, but these belonging genetically to Italian, "A"-population. Comparing Figures 5 and 7 one can find that south- westernmost coast of Norway is an important place of re-orientation of Blackcaps, while Scotland and Shetland Isles are not. Probably a flight from the Netherlands to Shetland Isles exhausts birds so much that they are not able to return the same way, or if they try, it is their last flight in life.

Most of the presented "strangers" go to or from Britain and it would be interesting to map starting places of their travels. These are mapped at Figure 8. In a case of recoveries of individuals ringed as full grown birds out of breeding season the localities cannot be treated as their home areas, but surprisingly they concentrate at quite limited area of central Europe.

Three presented above groups of "strangers" together show migration pattern very close to reverse "fan-shaped" pattern of normal migration of Central European Blackcap (Fig. 9). Note that W (and E) sectors are empty of recoveries of those "simple strangers". This could be an argument against Berthold and Terrill's (1988) hypothesis of western shift of normal migratory pattern. In these sectors however, can be found a few other strangers, which form an interesting group of recoveries. Three of them however, can be treated as "simple strangers" (Fig. 10), as their tracks point at vicinity of Caucasus, the area towards which migrate a few populations of European Passerines (e.g. Redwing, *Turdus iliacus* - Zink 1981, Rook, *Corvus frugilegus* - Busse 1969, 1986a). Occurrence of such Blackcap population is not yet documented by ringing recoveries, because its possible breeding area must be situated totally in Community of Independent States, at areas where is no ringing of small Passerines. Other recoveries of this group should be counted as "special strangers".

MIGRATION OF THE "SPECIAL STRANGERS"

The tracks of these individuals lead to nowhere from the point of view of migration to winter-quarters - their treatment both as normal and reverse passage do not point at any such area. Are they accidental deviations only? If one accepts the hypothesis, which leads to population pattern of the Blackcap presented at Figure 3, there is possibility of negative answer to that question. Most of the Central European Blackcaps are probably the interpopulational hybrids with inherited different programmes of migration, so it may be expected, they are able to navigate in different directions. E.g. an individual with inborn navigation programmes leading from Germany, its home area, to Spain and Italy (WA populations-hybrid) is able to navigate SW and S, but also NE and N respectively, when it "reads" the programme reversely.

Let us analyse behaviour of the migrant starting from somewhere in central Europe by track of reverse A navigation programme (Fig. 11A). It flew from the German coast NNW and after full night flight it landed at Norwegian coast. Next day it found that it was in wrong place - not closer, but farer from the goal (it is no point of discussing cues being a basis for such "conclusion"). Then the bird tries to correct the mistake and changes navigation programme (here "reversed A") into other one. If the individual has inherited only "A" (and, as we have seen, "reversed A") programme, it will start then to backward

fig.7

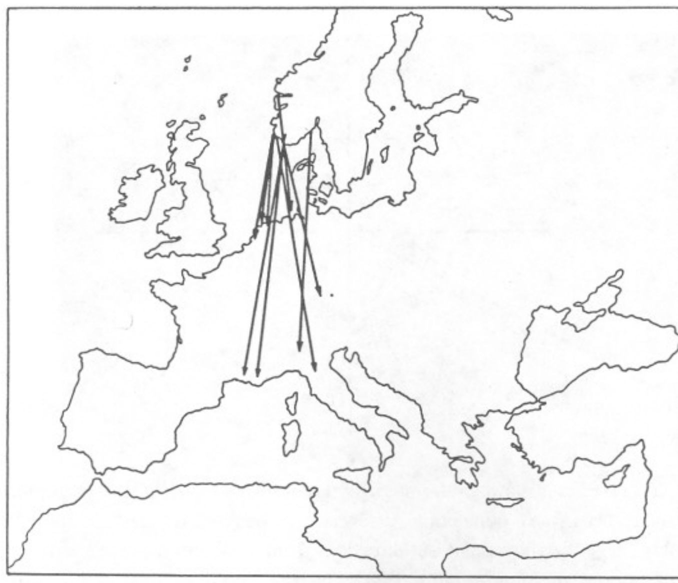


Fig. 7. "Strange" recoveries of Blackcaps - back reoriented A winter-quarter migration. Arrows mean the same as at Figure 4.

fig.8

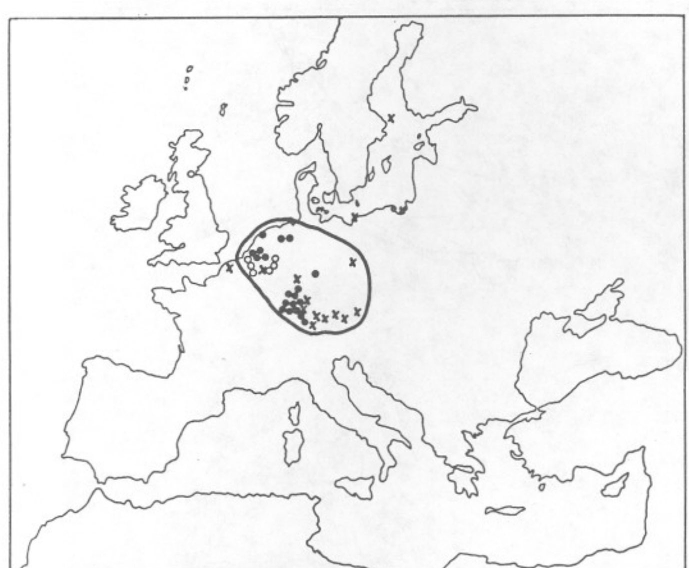


Fig. 8. Ringing localities of birds shown at Figures 4, 5 and 6 (reverse migration only). Symbols of groups as at these Figures.

fig.9

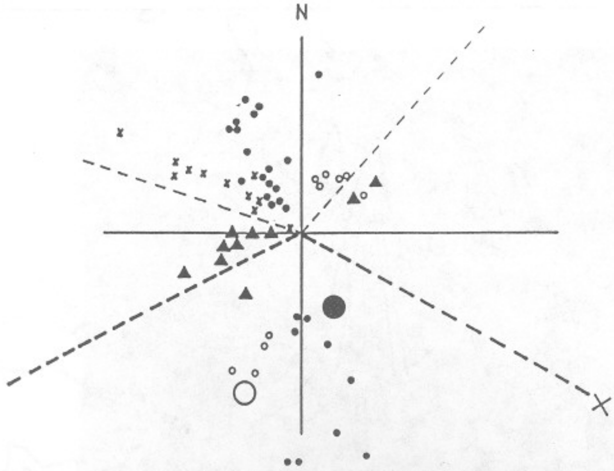


Fig. 9. Distribution of directions shown by the "strange" recoveries from Figures 4-7: ° - population W (reverse and backward tracks), • - population A (reverse and backward tracks), × - population B (reverse track only); bigger symbols point out directions from the centre of area shown at Figure 8 to the centres of appropriate winter-quarter. Border lines of normal and reverse migration recoveries are added. Symbols ∇ represent group called "special strangers".

fig.10

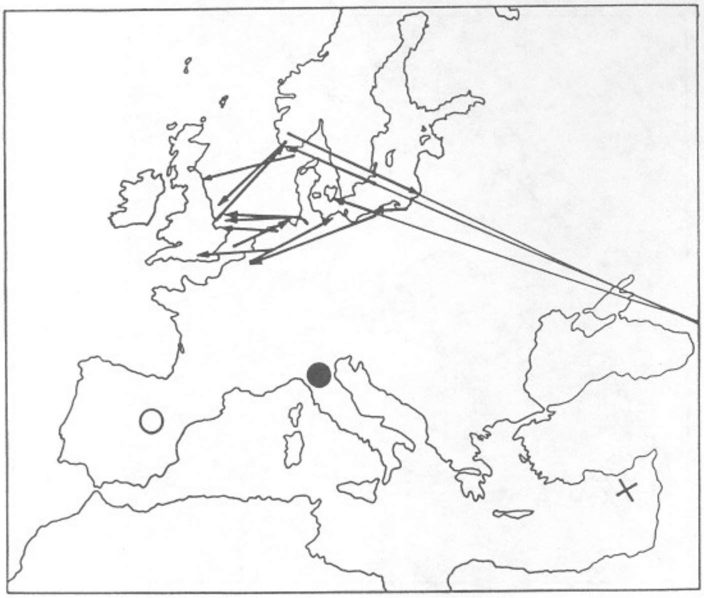


Fig. 10. "Special strange" recoveries of Blackcaps. Arrows mean the same as at Figure 4.

flight to German coast by A navigation track and, when ringed in Norway, produces one of recoveries shown at Figure 7 (being "simple strangers" only). However, when the inquired individual is the WA populations-hybrid, it has in its inherited "programme library" programmes "W" and "reverse W". If it chooses "W" programme, it flies across the North Sea and reaches in one of mornings British Isles as continental immigrant (Fig. 11A), where e.g. it is controlled at East Coast Bird Observatory. Then it is a potential British wintering bird. Note that in this story there is assumed the flight guided by inherited W-direction programme. It means that the bird flies along the track, which would lead it to W-area when the starting point of navigation would be at its natal area. Starting to programmed flight from another point the bird does not reach its primary goal. So, the hypothesis bases on assumed one-direction navigation system, which is usually true for young birds (a stock of immigrants is formed nearly exclusively by immatures). Basing on this assumption one is able to find the most probable, but, obviously, approximate place of the birds origin. Among eleven "special strangers" as much as six fit the hypothesis. Three further recoveries suggest that the birds have chosen reverse track programme (e.g. Fig. 11B) and last two ones can be explained by re-orientation to second of inherited correct directions, but the starting points of re- oriented flights were not at the place of ringing (Fig. 11C). The simpler explanation (as at Fig. 11A) would lead to an unacceptable localisation of natal area (in the case shown at Fig. 11C - in Italy, south of the Alps).

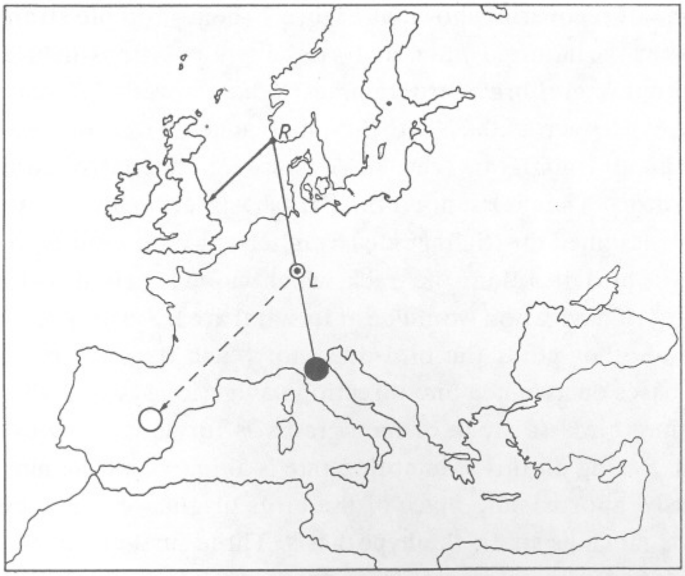
When examining these specially strange recoveries one does not know if studied individuals are WA, AB or WB- hybrids (in the recoveries inquired I have not found any WB one) so, all possibilities should be checked and more than one possible localisation may be found. In most cases, however, there is no doubt that some of them are very improbable, as laying far from the known areas of the mixed zones (e.g. at Fig. 11C).

THE NEW HYPOTHESIS: REVERSE MIGRATION MODEL OF BLACKCAP BEHAVIOUR

Summing up the results of analyses presented in last three chapters, one can list the main points of the hypothesis:

1. Most of continental immigrants to the British Isles reach this area by reverse track of normal migration directed to three winter-quarters. After arrival they reorient migration to backward track leading to proper winter-quarter,

fig. 11a



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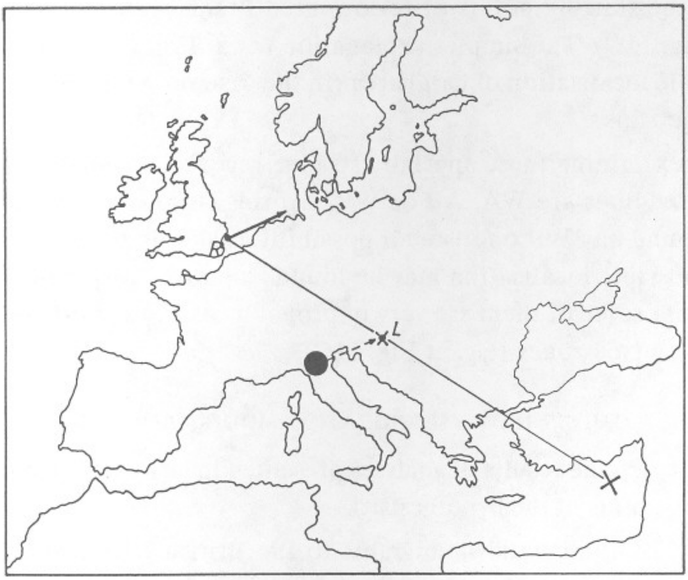

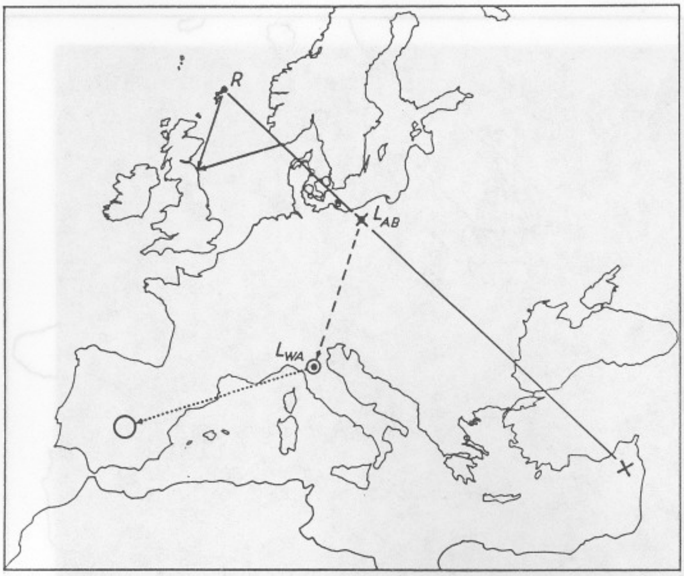

Fig. 11. Estimation of the origin of an individual which has given recovery represented by thick arrow. — - migration track prior to reorientation at locality "R", – - estimated reoriented track, L - estimated locality of origin. Symbols of populations as at Figure 3. A. WA- populations hybrid, reoriented W migration (reorientation at locality where ringed), B. AB-populations hybrid, reoriented to reverse A track at locality where ringed, C. AB-populations hybrid, reoriented at Shetlands (inprobability of reorientation to W direction at ringing place results from estimated locality of origin LWA).

departing in strictly opposite direction or, if they are interpopulational hybrids, change direction according to other inherited navigation programme.

2. Minority of immigrants already is at reoriented track, after reorientation at Norwegian coast of the North Sea.

The problem for discussion is: why the birds reorient their migration there after being on reverse track previously. Rabøl (1985) pointed that e.g. Yellow-browed Warblers, which reach Faeroes have navigated by reverse track during about 10 subsequent steps of migration without reorientation to correct navigation programme. It can be explained as follows: the bird migrating by reverse track over land does this at low level of stress as it can stop for a rest everywhere. This does not force the bird to control the position by other cues than accepted navigation programme (in discussed case - wrong, reverse track programme). A long flight over sea, frequently in unfavourable weather conditions, is a shock for

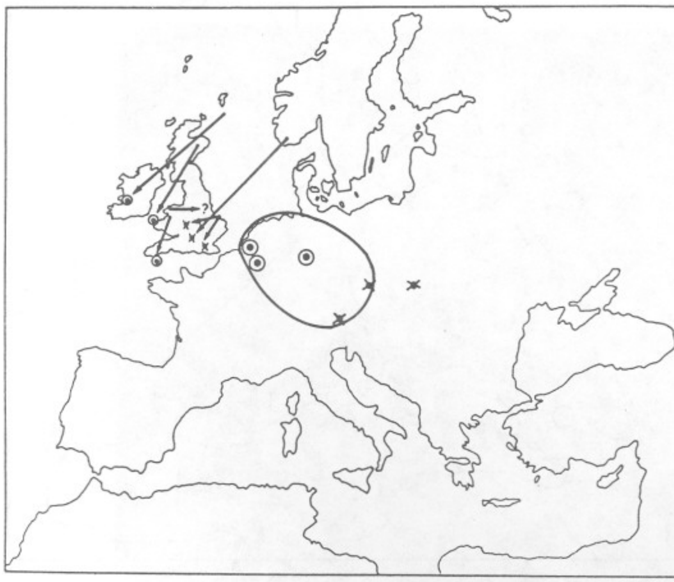

Fig. 12. Not local recoveries of Blackcaps wintering in Britain and Ireland. Estimated genetic characteristics of individuals and their natal localities are pointed by symbols: ⊙ - WA-hybrid, ✕- AB-hybrid. Area of origin of reverse migrants (Fig. 8) is shown.

the bird. This causes, if the individual finds land for stop, that the situation is reanalysed in light of all orientation cues included in complex orientation system of the species. The bird finds the error and tries to use other navigation programmes accessible in its inherited "library".

EXAMINATION OF THE BRITISH WINTERERS

Out of nine winter recoveries of Blackcap found on the British Isles (Langslow 1979, Mead and Clark 1988) out of place of ringing, two individuals were ringed on the Continent (Austria, Belgium) and they can be classified as "simple strangers" reaching Britain by reverse orientation track. The next six recoveries fit the group of interpopulational hybrids (three WA and three AB - Fig. 12), which suggests that stock of winterers contains mainly reoriented birds. This group of birds has travelled much greater distance than it could be expected comparing the position of known wintering area and probable area of origin. If one accepts the hypothesis described, it should be possible to check if conclusions resulting from it fit disposable information on winter distribution of Blackcaps in Britain and Ireland.

From the analysis of "strangers", it is known that main areas of reorientation

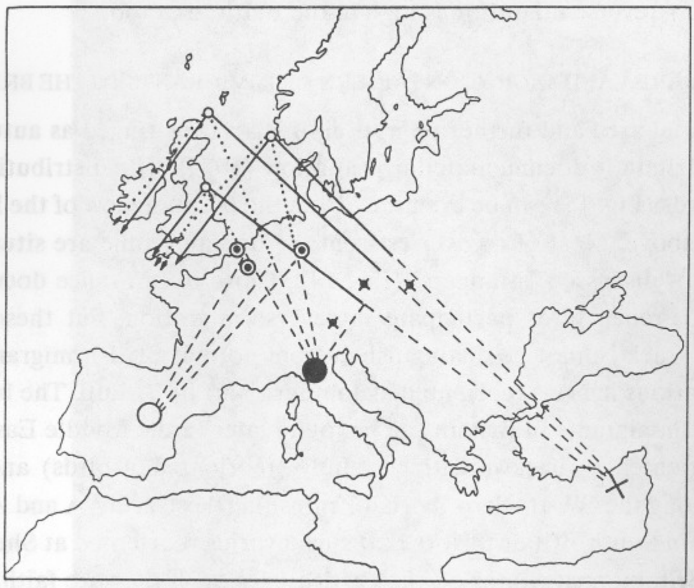

Fig. 13. Estimated the most probable tracks of migrants reoriented at Norway, Shetlands and north part of eastern coast, of which winterers are recruited. Assumed natal areas as found at Figure 12. In the window distribution of winterers is shown after Leach (1981).

of the Blackcaps being previously on reverse migration tracks are in south-west Norway, Shetlands and East Coast of Britain. At the latter area more in the north than in the south part of the coast (e.g. Williamson and Whitehead 1963). Starting from the natal areas of winterers found by examination of winter recoveries (Fig. 12) we may draw the most probable tracks of reoriented birds. The highest concentration of winterers on the British Isles should be expected along these tracks and it is so (Fig. 13).

THE NATAL AREA OF "STRANGERS" AND BIRDS WINTERING IN BRITAIN

Figure 12 shows that probable places of origin of British winterers lie mainly on the same area which was found for reverse migrants (Fig. 8). When we add localities found for "special strangers" as discussed earlier, the picture (Fig. 14) shows that the area covers nearly the whole known zone of interpopulation mixture (Fig. 3). This coincidence however, cannot be a basis for a conclusion that hybridisation leads to bigger instability of orientation system and tendency to reverse migration, because one must bear in mind that number of recoveries documenting reverse migration is high in the Baltic area too.

THE NATAL AREA AND MIGRATION PATTERN OF IMMIGRANTS TO THE BRITISH ISLES

The natal area and further migration of Blackcaps ringed as autumn immigrants to Britain is documentated by Langslow (1979). The distribution pattern of these birds (Fig. 15) can be examined from the point of view of the hypotheses presented above. Most of recoveries from the breeding time are situated at the natal area of discussed "strangers" (Fig. 14). Those from France document that number of French birds participate in reverse migration, but these being on reoriented track cannot be distinguished from normal British migrants and the WA populations hybrids reoriented at southern part of Britain. The birds ringed as autumn immigrants in Britain can be found later in the Middle East (B-birds, which reoriented to backward track), Italy (reoriented A-birds) and, in a big number, along the SW track to Iberian Peninsula (these are WA and AB-hybrids reoriented in South Britain). Note that such hybrids reoriented at Shetlands and northern Britain must winter on the British Isles or, if they are faithful to their second orientation programme, they must die in waves of the Atlantic Ocean. These latter ones are very strongly selected against. If, as it is shown in the papers of Leach (1981) and Berthold and Terrill (1988), the Blackcaps trying to winter inside British Isles have found there reasonable wintering place, they are intensively selected for. This difference in selection pressure is enough to force the growth in number of this part of Central European population, which have genetic tendencies to the reverse migration and their time-distance programme allows to stop migration on the British Isles.

The time-distance hypotheses

When one accepts Berthold and Terrill's hypothesis on western deviation of migration of Blackcaps wintering on the British Isles, it must be agreed that special mechanism of termination of migratory behaviour is involved. These authors assumed that inherited time-distance programme of migration is stopped by shorter days met by migrants. This hypothesis leads to conclusion that the birds originate from areas "approximately one third farther east than ringing returns, so far available". This conclusion however, is in contradiction with the area of origin found for British wintering birds when alternative hypothesis of migratory behaviour is accepted (Fig. 12, 14). So, it is necessary to reanalyse the problem. Figure 11 (A and C) shows that real distances covered by reorientated birds are much higher than it appears when comparing localities of natal and recovery

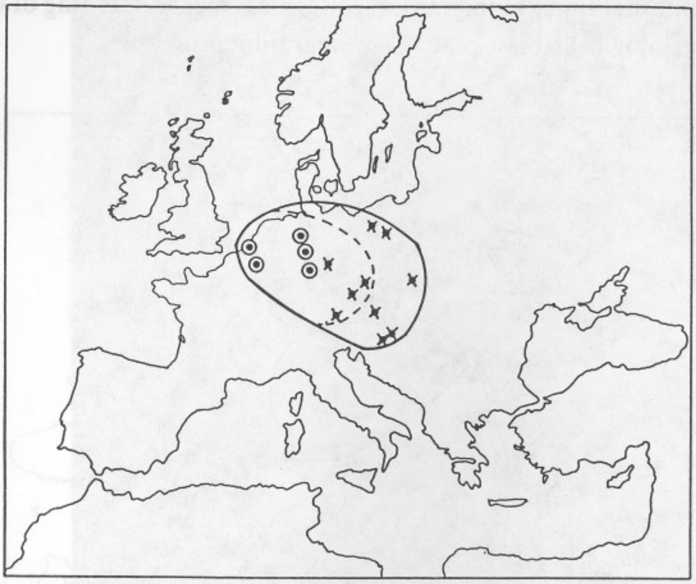

Fig. 14. Completed area of origin of Blackcaps immigrating to Britain and Ireland (area shown at Fig. 8 supplemented by estimated localities of origin of "special strangers" and winterers). Symbols as at Fig. 12.

places. E.g. the bird travel of which is shown at Figure 11A covered distance of about 1560 km instead of 780 km. If it started migration by correct "A"- programme and covered the same distance it would reach Sicily. Correct "W"-programme travel would end in Central Spain. Three of British winterers (Fig. 12) checked in the same way showed distances 1780, 2120 and 2660 km covered instead of apparent 780, 1580 and 2060 km, which would allow to reach Tunisia or S Spain, Cyprus or Algeria and Egypt or S of Sahara respectively. It shows that there is no necessary special mechanism stopping migration behaviour in Britain and Ireland. The last bird mentioned suggests, however, that even birds with inherited

Central Africa winter-quarter as a goal of migration can stop for winter in Britain. In that case finishing of migration in Britain by means of simple extinction of migratory restlessness seems to be doubtful as the distance covered by the bird is too short. Now, another possibility should be taken into consideration - probable relativity of the time counted by internal clock. The bird migrating by any internal time-distance programme hits an inherited goal of the travel when it flies under average conditions and along a track usual for population it belongs. In that case, run of the internal timer of migratory restlessness means counting of cumulative sums of physiological stresses caused by migration process.

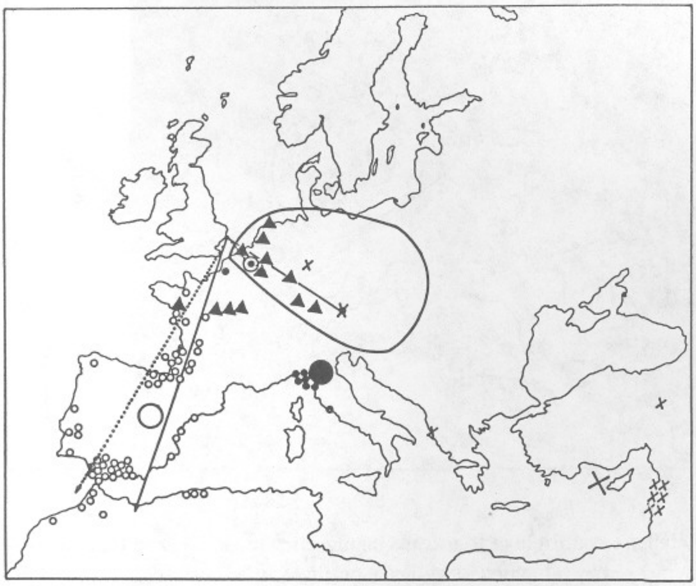

Fig. 15. Distribution of recovery places of Blackcaps ringed as autumn immigrants to Britain and recovered in the breeding season (*) and in migration/winter seasons (*). Estimated reoriented tracks (reorientation at south east) of WA and AB hybrids (originating from pointed localities at the area defined at Fig. 14) is shown (◉ - WA, ✕ - AB-hybrids).

Let us now examinate the timer of the bird which migrated by reverse direction-programme and covered long distance above sea and landed at dawn in Norway or Shetlands instead of e.g. Switzerland. The bird is exhausted by a long flight over the sea, it finds that it is in wrong place and it must reorient to one of alternative inherited programmes. So, the bird stays at place, but its timer counts high level of stress. In other words, the timer shows fictitious point in time-distance programme: the bird is physically late in relation to running programme, and it finishes migration before reaching the goal.

The hypothesis explained above should force experimentators to very cautious interpretation of orientation experiments carried out both on the birds living in constant, comfortable (as to nutrition and stress) conditions and those freshly caught at such places, where the birds arrive after a long and stressing flight. Evans (1968) studying passerines arriving from the North Sea to Northumberland found that in the first night after arrival only about 30% of individuals showed migratory restlessness, while then as much as 70% (the most active were heavier birds). Rabøl (1985) showed that some vagrants to Faeroes (being in situation clearly as described above) show different orientation during subsequent nights, trying different navigation programmes.

REVERSE MIGRATION MODEL AND FIELD EXPERIMENTS

Interpretation of results of field orientation experiments depends on models of navigation accepted by the student. When raw data are discussed, they are fitted to known models and the facts check the models. Usually some of the results do

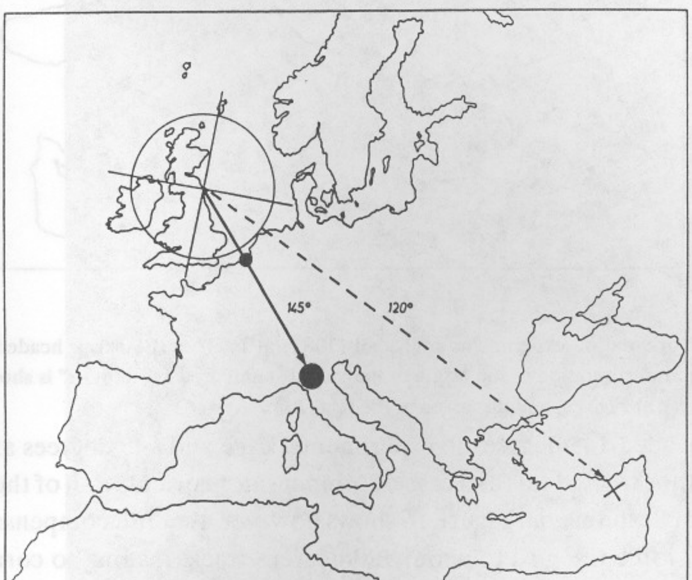

Fig. 16. Field orientation experiments by Evans (1968) in Northumberland. The Blackcap headed direction 145 degrees. Correct compensatory track to B-winter-quarter is drawn too.

not fit the models and they are treated as accidental deviations or they unexplainable facts. The reverse migration was taken into under consideration in some papers (e.g. Evans 1968, Wolff 1970, Rabøl 1985), but not discussed from the point of view presented in the model elaborated here. Usually the authors looked primarily for signs of compensatory orientation of vagrants being out of their normal migration track. The raw data presented there allow, however, to reanalyse some of the results obtained for Blackcaps checked for orientation after arrival to Northumberland and Faeroes respectively. The only individual studied

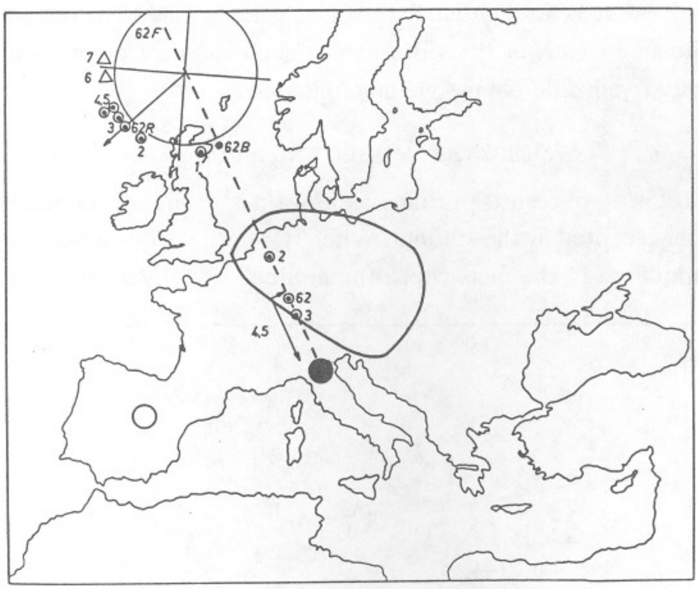

Fig. 17. Field orientation experiments by Rabol (1985) at Faeroes. Blackcap headed to directions shown. Interpretation of the origin of individuals numbered 1-7 and "62" is shown by symbols (as these at Fig. 12) and discussed in the text (p.).

by Evans headed 145 degrees in experimental cage and 145 degrees after release and the author treated this as a case of compensatory orientation of the individual drifted from Scandinavia. Figure 16 shows however, that full compensation of the drift would force the bird to about 120 degrees track, leading to correct goal of the population it belongs. 145 degrees track leads exactly to "A" winter-quarter in Italy, so the bird headed to reoriented backward track instead of assumed compensatory one. Rabøl (op. cit.) had at his disposal a few Blackcaps, of which one individual was tested twice (Fig. 17). The author stated that no compensatory orientation was found. In the light of reversed migration model he was right, but his calculation of mean track for all observed headings seems, from this point of view, to be wrong: the headings should be interpreted separately. The bird "1" was headed back to the area being in a range of dispersal of W population. Individual "62" being tested twice is of special interest: heading 62A is on a track back to Italy ("A"), while 62W is a track after reorientation to W- heading, what allows to estimate a place of the origin (being at area delimited as natal for immigrants to Britain). The birds "2", "3", "4" and "5" are reoriented ones too. The birds "6" and "7" were heading to nowhere, but their position is at half way between "62F" track (reversed, false direction of probable arrival) and reoriented direction close to "62W". Possibly, these birds are at a moment of disorientation during a change of navigation programmes.

Presented above different points of view on results of these field experiments stress an importance of clear distinguishing between two separate processes: compensation and reorientation. The former is a reaction of bird to wind-drift or human displacement and it heads to a track, which will lead to a goal of adopted navigation programme. E.g. an individual navigating by true "W" programme from Cornwall will hit Spain despite of easterly wind; it is possible that birds being on false track of reversed programme compensate deviations from that direction. Compensatory directions can be different, depending on magnitude of deviation. The second process, reorientation, is of another mechanism: it is a change of primarily applied navigation programme to quite another one, guiding the bird to a second goal of migration. The birds from pure population can choose only correct and reversed tracks: these starting by reverse one can reorient to backward ("correct") track only. The birds being interpopulational hybrids are able to navigate by four programmes (e.g. WA or AB hybrids) or more, if they are descendants of ancestors from more populations. An angle between tracks of arrival and departure from reorientation spot depends on inherited directions defined by localisation of natal area of the bird in relation to winter-quarters it is able to find.

CONCLUSIONS

The reverse migration model presented here, alternative to that of Berthold and Terrill's (1988) seems to fit well accessible data on Blackcap migration in the North Sea area. Further studies, especially by means of field orientation experiments and more intensive ringing are necessary.

The model should be checked on other species of passerines, as the phenomenon of mixed zones between different populations is observed in number of species and lot of continental immigrants to Britain may be on their reverse migration tracks instead of being drifted by wind as it is usually assumed.

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