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Between-species correlations in the number of migrants at Ulmethöchi (Switzerland)

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Abstract We analysed the number of autumn migrants at a bird ringing station over 41 years in the Jura mountains of Switzerland. For 12 irruptive or potentially irruptive bird species, the correlations between their numbers per year were calculated and the species were clustered accordingly. We found high correlations in the number of migrants between the Coal Tit *Periparus ater*, Great Tit *Parus major* and Blue Tit *Cyanistes caeruleus*. Most correlations of passage number between species pairs changed dramatically over time. Only Blue Tit and Coal Tit showed continuously high correlation in this respect. The variation and changes over time in between-species correlations in the number of migrants needs more attention.

Keywords Autumn migration · Correlation between the number of migrants of different species · Irruptive species · Partial migrants

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Introduction

Many short-distance migrants show marked among-year variation in their extent of autumn migration, including numbers migrating as well as the distance covered (for a review see Newton 2006). In more southern latitudes (e.g., central Europe) this phenomenon is reflected by the changing numbers of migrants coming from northern areas (e.g., Koenig 2001; Hüppop and Hüppop 2007; Korner-Nievergelt et al. 2007a). For some species extreme among-year variations can be observed, and such species are termed irruptive, though it remains a matter of definition where to set the limits.

A number of factors influencing the strength of autumn migration have been discussed, often focusing on species showing classical irruptions. Food availability in relation to population density is often seen as one key factor (Lack 1954; Koenig and Knops 2001; Newton 2006; Nilsson et al. 2006). Many of the typical irruptive bird species depend on tree fruits such as beech *Fagus sylvatica*, birch *Betula* sp., spruce *Picea abies* and pine *Pinus* sp. The crop size of these trees varies heavily among years (e.g., Svärdson 1957; Newton 2006). A good crop may reduce winter mortality of sedentary individuals and hence influence the population density of the following spring and summer positively (Flade and Schwarz 2004). Furthermore, good crop may allow boreal populations of finches (e.g., Red Crossbill *Loxia curvirostra*, Common Redpoll *Carduelis flammea*, Eurasian Siskin *Carduelis spinus*) to produce an additional brood (preceding the regular brood; Svärdson 1957) or, in the case of nomadic species such as Red Crossbill, may prompt flocks coming from further north or east to settle (Svärdson 1957). Large mass movements have often been observed when such a good crop year and, hence, a population increase was followed by food shortage in autumn or winter (Perrins 1966; Heldbjerg and Karlsson 1997; Koenig and Knops 2001; Newton 2006). The proximate role of abiotic environmental factors such as rainfall and temperature, on the other hand, seems to be more ambiguous, with some authors claiming their influence to be of little importance (van Balen and Hage 1989; Koenig and Knops 2001) while others found at least some influence (Nilsson et al. 2006; Sæther et al. 2007). Jenni (1987) showed that extensive snow cover forces Bramblings *Fringilla montifringilla* to move south.

Ecologically similar species are expected to show some synchrony in the yearly variation of the number of migrants. While earlier works often failed to find synchrony among species (Lack 1954; Ulfstrand 1963), more recently, certain correlations became evident, potentially due to the larger datasets that gradually became available. The Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major*, that both feed on beech seed, tend to irrupt in the same years, and the irruptions of Red Crossbills and Great Spotted Woodpecker *Dendrocopos major*, both feeding on spruce seed, were correlated (Newton 2006). Bock and Lepthien (1976) showed that irruptions of eight boreal seed-eating bird species were synchronised to some extent, especially in eastern North America. Larson and Bock (1986) and Koenig (2001) also found synchronous irruptions. Interestingly, both noted that the degree of synchrony can vary strikingly through time.

Here, we analysed 41 years of bird-ringing data collected on a hill pass in the Jura mountains of northern Switzerland. Due to the highly standardised catching effort, numbers caught per species can be compared across the years and allow us to investigate the correlations between migrant numbers in different species. We mainly focused on species showing high among year variations in numbers, i.e., species classically known to be irruptive. Our objectives are describing correlations in the number of migrants between species, and analysing long-term changes of these correlations.

Methods

Species and ringing activity

Since 1966, birds were regularly caught and ringed at Ulmethöchi (973 m asl, Jura mountains, northwestern Switzerland, Canton Basel-Landschaft) during autumn migration (Korner-Nievergelt et al. 2007a). Birds were caught using a total of 150 m of mist nets. Ringing was done according to the guidelines of the Swiss Ornithological Institute in Sempach. The position of the nets remained essentially unchanged through all years, and the surrounding landscape did not change markedly, e.g., a hedge in the catching area was regularly cut to the same height and the forest and meadow mosaic in the area remained constant.

For this work, data from the time period of 27 September through 22 October and the years 1966 through 2006 were available. Ringing took place on all days during this period except for 1967 (1 day without ringing), 1968 (3), 1970 (6), and 1974 (1), and except during heavy rain, when no birds were passing.

The 12 species listed in Table 1 are essentially those passeriformes known to perform irruptions in central Europe (Winkler 1999), and which we caught regularly ($n \geq 50$). We only included species whose median passage

Table 1 Total number of individuals caught during the observation period of the studied species at Ulmethöchi, Jura mountains, Switzerland, between 1966 and 2006, number of irruptions (irruption = number caught $\geq 2 \times$ 7-year average), and the range of the five lowest and five highest numbers of birds caught during one observation season, i.e., between 27 September and 22 October

Species	Total number of individuals	Number of irruption (years)	Range of five lowest numbers	Range of five highest numbers
Goldcrest *Regulus regulus*	1,139	6	1–4	57–157
Marsh Tit *Parus palustris*	161	3	0–1	8–14
Coal Tit *Periparus ater*	5,894	7	2–10	491–823
Blue Tit *Cyanistes caeruleus*	6,576	7	8–29	383–916
Great Tit *Parus major*	6,675	7	4–16	514–537
Eurasian Jay *Garrulus glandarius*	453	8	0–0	45–98
House Sparrow *Passer domesticus*	60	11	0–0	3–11
Eurasian Tree Sparrow *Passer montanus*	74	7	0–0	5–15
Common Chaffinch *Fringilla coelebs*	16,233	0	58–147	742–1,103
Eurasian Siskin *Carduelis spinus*	6,361	6	0–26	417–669
Common Linnet *Carduelis cannabina*	153	8	0–1	9–16
Hawfinch *Coccothraustes coccothraustes*	261	8	0–0	22–42

day fell within our observation period (for this reason, Nuthatch *Sitta europaea*, Brambling and Eurasian Bullfinch *Pyrrhula pyrrhula* were excluded). The median passage days were taken from Gatter (2000), whose data were based on 18 years (1970–1987) and an observation period from 15 July to 15 November at Randecker Maar, 200 km to the NE of Ulmethöchi. Some species generally not treated as irruptive have been added in our analysis because their numbers at Ulmethöchi fluctuated heavily (Goldcrest *Regulus regulus*, House Sparrow *Passer domesticus* and Eurasian Tree Sparrow *Passer montanus*; Korner-Nievergelt et al. 2007a), or to allow comparisons between congeneric irruptive and non-irruptive species (Marsh Tit *Parus palustris* and Common Linnet *Carduelis cannabina*).

Methodological aspects

Our observation period of 4 weeks is relatively short. However, migration peak of each species included in the study was during our observation period. Also, comparing irruption years of seven species (Blue Tit, Great Tit, Coal Tit, Marsh Tit, Jay, Siskin, Hawfinch) with the station Randecker Maar (see above), where the entire migration period was covered, a good agreement was found (data not shown). This indicates that our data are a valid measure of the numbers passing through.

In our analysis, we clustered species according to their correlations in their number of migrants per year (see below). Because the local weather has a strong effect on the number of birds passing, species that pass during the same period (within year) will tend to cluster. This could be a problem especially if species migrating at very different times per year are included. However, we only included species migrating relatively late. Furthermore, we analysed whether species-pairs with similar median passage days (from Gatter 2000) correlated better than species-pairs with more different median passage days. We found that there was no such relationship, i.e., there was even a weak tendency in the opposite direction (linear regression, $\beta = 0.009$, $p = 0.08$, $R^2 = 0.04$; Fig. 1). Note that the low R^2 indicates a very poor relationship.

Statistical analysis

We used the mean number of individuals caught per day and per species and averaged this number for each year. This is essentially equivalent to taking year-totals per species, but corrects for the slight variation of ringing effort over the years (4 years with a few days missing, see above). The mean day-totals per species and year were log-transformed. We then used the residuals of a linear regression of these values against year to remove long-term trends. This is crucial, because otherwise the numbers of

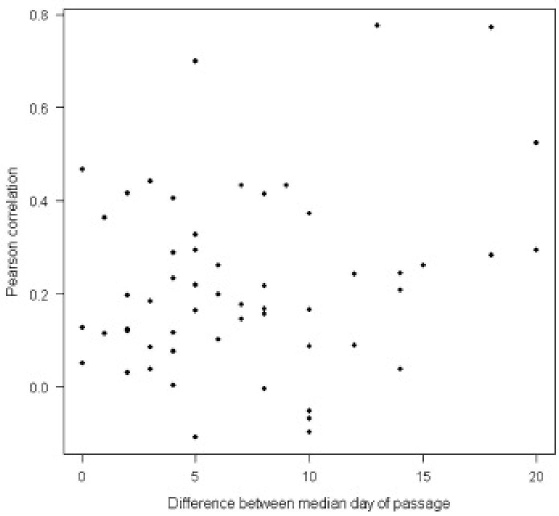

Fig. 1 Relationship between the difference of median passage day (from Gatter 2000) and the correlation of the number of birds caught (log-transformed, detrended and scaled) for all possible species pairs (*dots* 12 species in the analysis)

species which showed the same long-term trend would necessarily be correlated.

For each species, years with more than double the number of individuals caught compared with its 7-year average (mean of $t-3$, $t-2$, ..., $t+2$, $t+3$) were defined as irruption years, all others as normal years.

We performed an agglomerative hierarchical cluster analysis based on the correlations between the mean daily totals of the species (Kaufmann and Rousseeuw 1990). In this procedure, the species with the highest correlations are first grouped together. Thereafter, species or groups with the highest correlation with the means of the first group are added sequentially. This analysis produces a tree diagram where species with a similar pattern of numbers caught over the years lay close to each other. Also, approximately unbiased p_{boot} values for each cluster were calculated based on 100,000 multiscale bootstrap replicates (Shimodaira 2004). These p_{boot} values indicate how strong the cluster is supported by the data. Clusters with p_{boot} values higher than 95% are strongly supported.

We also performed a second cluster analysis based on the "yes/no" criterion of irruptions as defined above. As a linking method, we used Ward's method based on binary distances (Becker et al. 1988). The resulting tree was similar to the tree produced by the mean daily total numbers. The same tit-cluster was produced with both methods, while the grouping of the other species was not significant. Due to the similarity of the two trees in the essential parts we do not present the tree based on the "yes/no" criterion of irruption.

All statistical analysis were done using R 2.5.0 (R Development Core Team 2006).

Results

The species included in this analysis showed large among-year variation in numbers caught (Table 1; Fig. 2). The cluster analysis based on the correlations between the yearly migrants over the period of 1966–2006 revealed a strong association of the three tit species: Coal Tit, Great Tit and Blue Tit ($p_{boot} = 100\%$; Fig. 3). Furthermore, an association trend ($p_{boot} = 90\%$) among the House Sparrow, Linnet, Chaffinch, Marsh Tit and Tree Sparrow could be seen.

The correlation of numbers of birds caught between species varied considerably with time. Correlations between pairs of species for moving 15-year intervals between 1966–1981 and 1992–2006 varied from −0.15 to 0.90 (Fig. 4). We compared species-pairs that associated at least during one 15-year period in the cluster analysis (Fig. 5). Only the pair Blue tit–Coal Tit showed relatively constant and high correlations over the 41 years. The numbers of Goldcrest and Hawfinch were slightly correlated during the period 1971–1993, whereas before and after this period the correlation did not reach the level of significance. A similar development over time is seen in the correlation between the Siskin and the Coal Tit. The number of Goldcrests was independent of the number of House Sparrows until the 1980s, when this correlation dramatically increased (from 0 to 0.7).

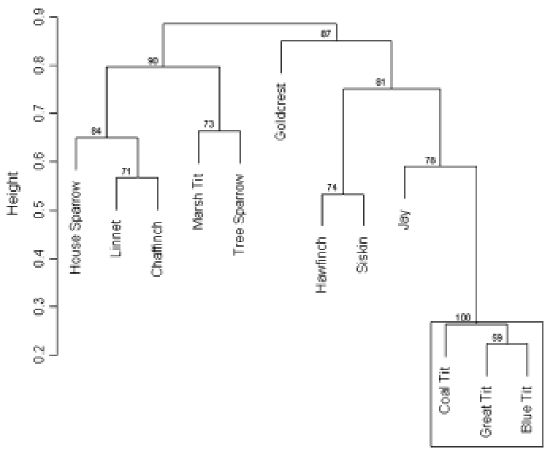

Fig. 3 Grouping of the species according to the correlation of their yearly numbers (log-transformed, detrended and scaled) caught at Ulmethöchi over 41 years. Species on the same branch in the tree showed high correlations of their numbers caught. Numbers at the nods indicate the bootstrap approximately unbiased p_{boot} values (100,000 replicates): Higher values indicate more confident groups. The *box* indicates the significant group (p_{boot} value > 95%)

Accordingly, tree diagrams based on different 15-year intervals changed over the 41 years (Fig. 5). Blue and Coal Tit clustered together in all three time periods, whereas for the other species the clustering changed significantly. Note that the larger bootstrap values in the dendrograms based on 15 years compared to the one based on 41 years (Fig. 3) are, at least partly, a consequence of including fewer years, which makes clustering more univocal.

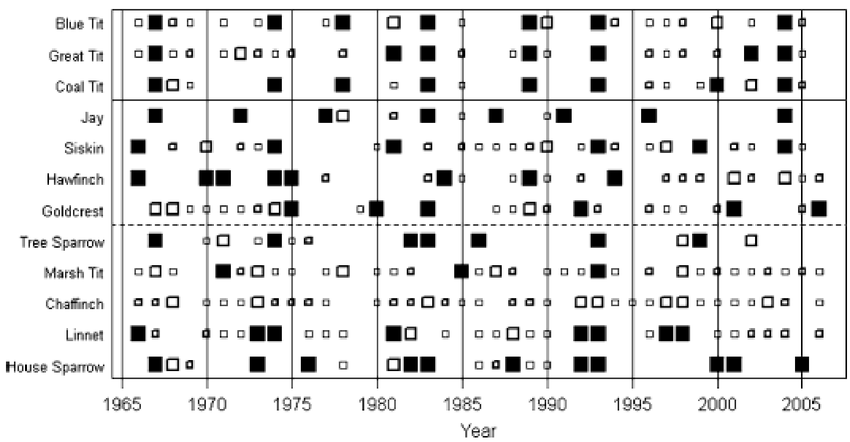

Fig. 2 Number of migrants for 12 species at Ulmethöchi classified in five classes: *no sign* = lower than 0.5 of the 7-year average, *small open rectangular* = lower than the 7-year average but higher than 0.5 this mean, *small bold rectangular* = between the 7-year average and 1.5 times this mean, *large bold rectangular* = between 1.5 times the 7-year average and twice this average, *large filled rectangular* = more than the 7-year average. Species are ordered according to the cluster analysis from Fig. 3. The *solid horizontal line* separates the highly correlated tit-species and the *broken line* divides the species into two groups that were adumbrated by the cluster analysis (see Fig. 3)

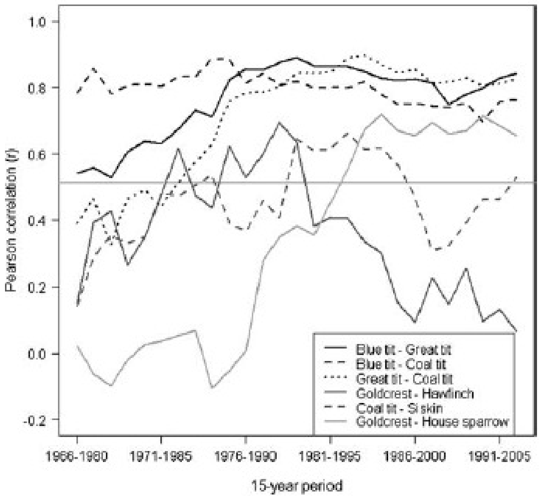

Fig. 4 Long-term changes of correlations between selected species-pairs based on the yearly total number of birds caught at Ulmethöchi for a moving 15-year time-window between 1966 and 2006. Depicted are species-pairs of groups with high bootstrap values in Fig. 3 and 5. *Horizontal grey line* 5% significance level

Discussion

As expected, species generally classified as irruptive showed strong among year variation in their numbers passing across Ulmethöchi, northern Switzerland (Table 1). Irruption years, here defined as more than twice the moving 7-year average, are depicted in Fig. 2 (large filled rectangles). This figure allows directly comparing among species and it is visible that the tit species produced strong numbers often in the same years.

With our short observation period of 4 weeks, it is likely that we missed some irruptions of the species we analysed, though we believe that we registered the majority of irruptions for the following reasons. First, we included only species whose peak of migration lay within our observation period. Secondly, comparing our irruptions with those registered 200 km to the NE (at Randecker Maar, Gatter 2000), where the entire migration season is registered and which lies in the direction most birds at Ulmethöchi come from, showed a good agreement (7 species could be compared, 78% analogy in the classification of years as irruption and non-irruption years).

Classification of irruption years is a matter of definition, and it only allows binary comparisons. Therefore, our main analysis looked at the numbers passing. The correlation in the numbers passing between the species was used to produce a dendrogram (Fig. 3), which also allows estimation of significance values. The cluster analysis confirmed the correlations between the tits while all other groups show trends only, at the best.

Extreme weather situations lasting the entire observation period can similarly affect the number of all migrating species. While this does not affect the configuration of the species on the dendrogram, it tends to inflate the value of the correlations. In order to assess the influence of this effect, we also performed the cluster analysis based on the year-wise rank of the number of migrants instead of the absolute values. As the rank is a relative measurement, it is independent of the overall level of migration intensity. This cluster analysis gave essentially the same result as the one based on the absolute number of migrants although the p_{boot} values were lower (68–88%): Blue and Coal Tits were again found on the same branch and loosely associated with the Great Tit and the Jay (p_{boot} value 83%). Furthermore, the tree based on the binary data, irruption year versus normal year (which is a very robust measure of abundance), gave, again, a similar tree, with the Blue and Coal Tit clustering together with a p_{boot} value of 98%, and the Great Tit associated with them (87%), whereas all other species did not cluster. Because of the similarities between the cluster analysis based on absolute values of the number of migrants and the ones based on relative numbers (rank, binary), we conclude that the correlations we found were not significantly inflated by extreme weather situations.

In our data, the highest (and significant) correlations were observed among the three tits known to show irruptions relatively often, i.e. Coal Tit, Great Tit and Blue Tit. Schüz (1971) wrote that the number of migrating Blue and Great Tits correlated at the Courish spit, while Coal Tits correlated with Great Spotted Woodpecker and Red Crossbill, all spruce seed eaters in the north. However, Schüz (1971) also cited observations from The Netherlands, where Coal Tits heavily depended on caterpillars. This illustrates that irruptions and their triggering factors may vary between sites of observation. Furthermore, it seems likely that, depending on the species, irruptions may be more influenced by autumn and winter food, such as tree mast, or by spring food availability influencing breeding success. Much more about the provenance of our migrants and their food requirements through the year needs to be known to safely interpret our observed pattern. As a working hypothesis, we suggest that good breeding conditions allows all three tit species, notably species producing large and multiple clutches, to strongly increase their population sizes. This in turn creates the potential for an irruption. Regarding this last component, several studies have concluded that population size might trigger irruptions in these three tit species (Berndt and Henss 1963, 1967; Schüz 1971; Brotons 2000; Markovets and Sokolov 2002; Newton 2006).

For most species-pairs, their correlation of the yearly numbers fluctuated heavily among time periods (Fig. 4). Correspondingly, data of different 15-year periods produced

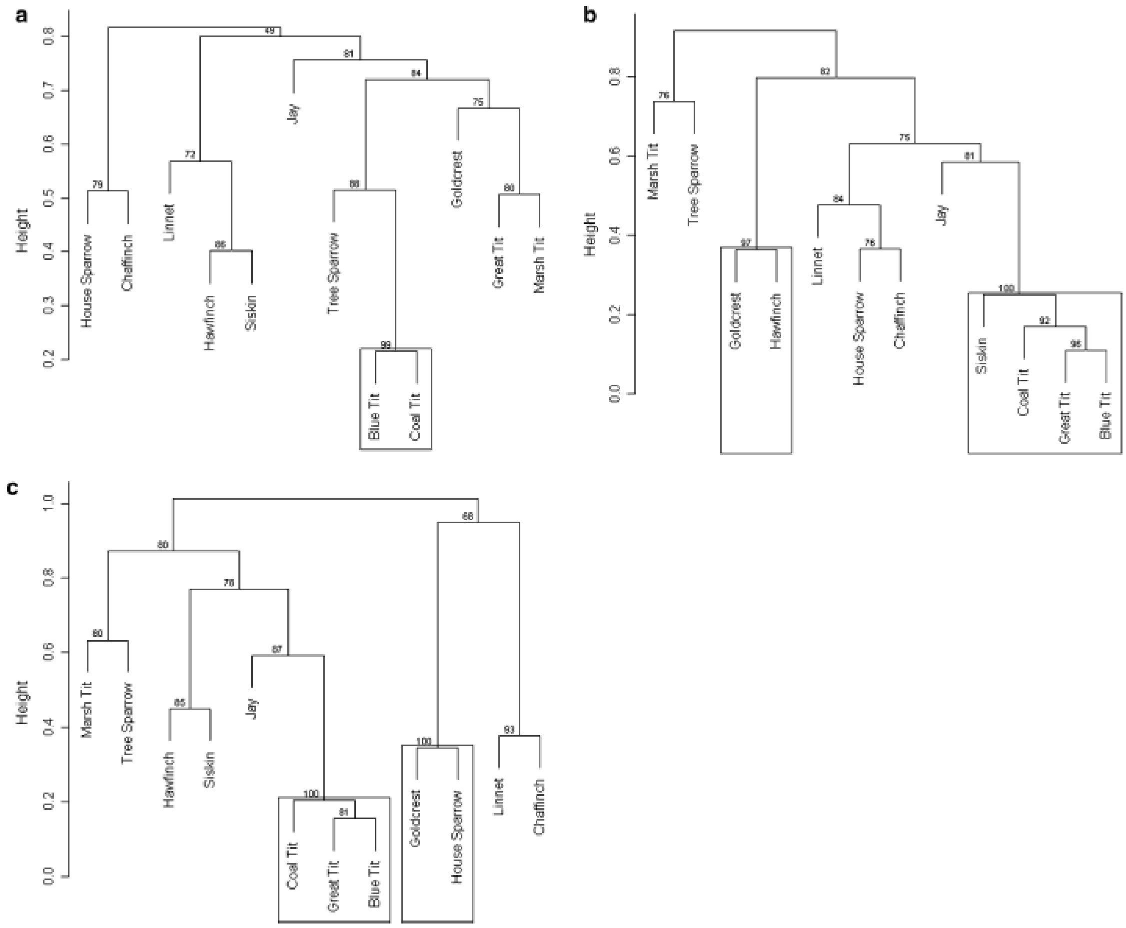

Fig. 5 Dendrograms based on cluster analysis of number of birds caught per year, separately for three 15-year intervals: a 1966–1980, b 1979–1993, c 1992–2006. See caption of Fig. 3 for details

different dendrograms (Fig. 5). Similar fluctuations have been described by Larson and Bock (1986) and Koenig (2001). We agree with Koenig (2001) that better knowledge of these dramatic temporal shifts may be critical for understanding synchrony in eruptions and passage numbers in general. Potentially, years exceptional in some key parameter (e.g., weather factors, parasites) synchronise key food plants or animals (e.g., the fructification of certain trees, or prey animals for nestling feeding) across a large area. This synchrony may then decline gradually over the years. In parallel, bird species thus appear in similar numbers for some years, but low correlations are found in others. The only exception we found was the Blue tit–Coal Tit species pair, which correlated well over the entire observation period (Fig. 4) and was constantly in the same cluster (Fig. 5). For one thing, the observation of fluctuating synchrony suggests that it is not possible to extrapolate an observed correlation based on a relatively short time period (e.g., 15 years) to a generally valid statement about a species-pair. More interestingly, fluctuating synchrony in migration intensity seems to be a characteristic of short distance migration and requires an explanation.

In future, it might be valuable to conduct comparative analysis similar to the one of Brotons (2000) by including several species for examining the relation of migration strategy, winter ecology, diet, and demographic parameters with irruptive behaviour. Furthermore, a comprehensive analysis of now gradually becoming available long-term data sets of different bird migration stations spread over a large area would be valuable to illuminate long-term changes of geographic patterns and spatial correlations of irruptions.

In conclusion, we found that the number of migrants of the Coal Tit, Blue Tit and Great Tit were highly correlated over 41 years. The correlations in the numbers of migrants can change dramatically over time, a phenomenon that needs much more attention in future work on passage number synchrony.

Zusammenfassung

Korrelationen zwischen Arten in der Zahl der Durchzügler auf der Ulmethöchi (Schweiz)

Aus Durchzugszahlen im Herbst berechneten wir die Korrelationen zwischen 12 Invasions- oder potenziellen Invasionsarten und führten aufgrund der Korrelationen in den Fangzahlen eine Clusteranalyse durch. Die Vögel wurden während 41 Jahren unter den gleichen Bedingungen auf der Beringungsstation Ulmethöchi auf einem Passübergang im Jura, Kanton Basel-Landschaft, Schweiz, während des Herbstzuges gefangen. Über die 41 Jahre gruppierten sich Tannen-, Kohl- und Blaumeise signifikant. Wird die Clusteranalyse für drei 15-Jahresabschnitte (1966–1980, 1979–1993 und 1992–2006) separat durchgeführt, so unterscheiden sich die identifizierten Gruppen stark. Nur die Blau- und Tannenmeise befanden sich in allen drei Zeitabschnitten in derselben Gruppe. Entsprechend zeigten die für gleitende 15-Jahresintervalle von 1966–2006 berechneten Pearson's Korrelationsindices nur für das Artenpaar Tannenmeise-Blaumeise kontinuierlich hohe Werte. Die Korrelation in der Anzahl Fänglinge variierte für andere Artpaare stark, wobei für einzelne Zeitabschnitte signifikante Korrelationen auftreten können: Ein Effekt, welchem in Zukunft bei Studien über die Synchronie von Irruptionen mehr Aufmerksamkeit geschenkt werden sollte. Die starke Korrelation in den Fangzahlen zwischen Kohl-, Tannen- und Blaumeise kann erst sicher interpretiert werden, wenn Herkunft und Nahrungsverhalten im Jahresverlauf unserer Meisen bekannt sind. Als Arbeitshypothese schlagen wir vor, dass besonders gute Brutzeitbedingungen die Populationen dieser sehr produktiven Arten stark anwachen lassen und so das Potential für Massenemigration schaffen.

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References

Becker RA, Chambers JM, Wilks AR (1988) The new S language. Wadsworth & Brooks/Cole, Wadsworth

Berndt R, Henss M (1963) Die Blaumeise, *Parus c. caeruleus* L., als Invasionsvogel. Vogelwarte 22:93–100

Berndt R, Henss M (1967) Die Kohlmeise, *Parus major*, als Invasionsvogel. Vogelwarte 24:17–37

Bock CE, Lepthien LW (1976) Synchronous eruptions of boreal seed-eating birds. Am Nat 110:559–571

Brotons L (2000) Winter territoriality and irruptive behavior in the Paridae. Auk 117:807–811

Flade M, Schwarz J (2004) Ergebnisse des DDA-Monitoring-programms, Teil II: Bestandsentwicklung von Waldvögeln in Deutschland 1989–2003. Vogelwelt 125:177–213

Gatter W (2000) Vogelzug und Vogelbestände in Mitteleuropa. Aula Verlag, Wiebelsheim

Heldbjerg H, Karlsson L (1997) Autumn migration of Blue Tit *Parus caeruleus* at Falsterbo, Sweden 1980–94: population changes, migration patterns and recovery analysis. Ornis Svec 149:149–167

Hüppop K, Hüppop O (2007) Atlas zur Vogelberingung auf Helgoland, Teil 4: Fangzahlen im Fanggarten von 1960 bis 2004. Vogelwarte 45:145–207

Jenni L (1987) Mass concentrations of Bramblings *Fringilla montifringilla* in Europe 1900–1983: their dependence upon beech mast and the effect of snow-cover. Ornis Scand 18:84–94

Kaufmann L, Rousseeuw PJ (1990) Finding groups in data. Wiley, N.J.

Koenig WD (2001) Synchrony and periodicity of eruptions by boreal birds. Condor 103:725–735

Koenig WD, Knops JMH (2001) Seed-crop size and eruptions of North American boreal seed-eating birds. J Anim Ecol 70:609–620

Korner-Nievergelt F, Korner-Nievergelt P, Baader E, Fischer L, Schaffner W, Kestenholz M (2007a) Herbstlicher Tagzug auf der Beringungsstation Ulmethöchi im Jura: Veränderungen in den Fangzahlen über 40 Jahre (1966–2005). Ornithol Beob 104:3–32

Korner-Nievergelt F, Korner-Nievergelt P, Baader E, Fischer L, Schaffner W, Kestenholz M (2007b) Jahres-und tageszeitliches Auftreten von Singvögeln auf dem Herbstzug im Jura (Ulmethöchi, Kanton Basel-Landschaft). Ornithol Beob 104:101–130

Lack D (1954) The natural regulation of animal numbers. Clarendon Press, Oxford

Larson DL, Bock CE (1986) Eruption of some North American boreal seed-eating birds, 1901–1980. Ibis 128:137–140

Markovets MY, Sokolov LV (2002) Spring ambient temperature and movements of Coal Tits. Avian Ecol Behav 9:55–62

Newton I (2006) Advances in the study of irruptive migration. Ardea 94:433–460

Nilsson ALK, Lindström Å, Jonzén N, Nilsson SG, Karlsson L (2006) The effect of climate change on partial migration—the blue tit paradox. Glob Chang Biol 12:2014–2022

Perrins CM (1966) The effect of beech crops on Great Tit populations and movements. Br Birds 59:419–432

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.r-project.org

Schüz E (1971) Grundriss der Vogelzugkunde. Parey, Berlin

Shimodaira H (2004) Approximately unbiased tests of regions using multistep-multiscale bootstrap resampling. Ann Stat 32:2616–2641

Svärdson G (1957) The "invasion" type of bird migration. Br Birds 50:314–343

Sæther B-E, Engen S, Grøtan V, Fiedler W, Matthysen E, Visser ME, Wright J, Møller AP, Adriaensen F, van Balen H, Balmer D, Mainwaring MC, McCleery RH, Pampus M, Winkel W (2007) The extended Moran effect and large-scale synchronous fluctuations in the size of Great tit and Blue tit populations. J Anim Ecol 76:315–325

Ulfstrand S (1963) Ecological aspects of irruptive bird migration in Northwestern Europe. Proc Int Ornithol Congr 13:780–794

van Balen JH, Hage F (1989) The effect of environmental factors on tit movements. Ornis Scand 20:99–104

Winkler R (1999) Avifauna der Schweiz. Ornithol Beob Beiheft 10:252