

## The Microevolution of Migratory Behaviour in the Blackcap: Effects of Genetic Covariances on Evolutionary Trajectories

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**SUMMARY** - Phenotypic evolution may be constrained by the lack of genetic variation or by unfavourable genetic correlations. While the amount of additive genetic variance determines the rate of evolutionary change, genetic covariances may influence the evolution of a suite of characters by counteracting selection, thus retarding adaptive changes, or by reinforcing selection responses. We studied the quantitative genetics of incidence, amount, onset, intensity, and termination of autumn migratory restlessness in the Blackcap (*Sylvia atricapilla*) with the aim of identifying potential genetic constraints on the direction and rate of evolutionary change in migratory behaviour. Drawing on data from two Blackcap populations, one a completely and the other a partially migratory population, we assessed genetic variances and covariances using midparent-offspring regressions, or from responses to artificial selection. We found high phenotypic variation and significant heritabilities for incidence, onset, intensity and amount of migratory activity, demonstrating high evolvability of these traits. Termination of autumn migration, however, has a low heritability. Moreover, we found a genetic correlation not significantly different from 1 between incidence and amount of migratory activity, suggesting that both characters are different aspects of the same trait. The proportion of migrants in a population thus is determined by the distribution of migratory activities in the population and a population specific threshold. High genetic correlations among all behavioural traits indicate that migratory traits in the Blackcap are expressed as a genetically integrated syndrome. Selection on any of these traits will induce changes in all other traits. The signs of the genetic correlations among migratory traits are in accord with interspecific correlation patterns, and may reinforce the response to selection imposed by global warming.

**RIASSUNTO - La microevoluzione del comportamento migratorio nella Capinera: effetti delle covarianti genetiche sulle traiettorie evolutive.** L'evoluzione del fenotipo può essere limitata dalla mancanza di variabilità genetica o da correlazioni genetiche sfavorevoli. Se la quantità di varianza genetica additiva determina il tasso di mutamenti evolutivi, le covarianti genetiche possono influenzare l'evoluzione di una serie di caratteri contrastando la selezione, e quindi ritardando i mutamenti adattativi, o rinforzando i processi selettivi. Abbiamo studiato la genetica quantitativa dell'incidenza, quantità, inizio, intensità e termine dell'irrequietezza migratoria autunnale nella Capinera (*Sylvia atricapilla*) al fine di identificare potenziali limiti nella direzione e nel tasso dei mutamenti evolutivi nel comportamento migratorio. Sulla base di dati relativi a due popolazioni di Capinera, una completamente e l'altra parzialmente migratrici, abbiamo valutato varianti e covarianti genetiche utilizzando relazioni genitori-prole, o in base a risposte a selezione artificiale. Abbiamo riscontrato un'alta variabilità fenotipica e tassi significativi di ereditabilità per quanto concerne l'incidenza, l'inizio, l'intensità e la quantità di attività migratoria, dimostrando l'alto potenziale evolutivo di questi tratti. La conclusione della migrazione autunnale mostra però bassi tassi di ereditabilità. Abbiamo inoltre riscontrato una correlazione genetica non significativamente diversa da 1 tra incidenza e quantità di attività migratoria, il che suggerisce che i due caratteri siano aspetti diversi dello stesso carattere. La proporzione di individui migratori in una popolazione è quindi determinata dalla distribuzione delle attività migratorie nella popolazione e da un livello di soglia specifico per la popolazione stessa. Alte correlazioni genetiche tra tutti i tratti comportamentali indicano che le caratteristiche migratorie della Capinera sono espresse quali sindrome integrata su base genetica. La selezione a carico di qualunque di questi tratti indurrà mutamenti anche in tutti gli altri. I segnali delle correlazioni genetiche tra le caratteristiche migratorie sono in accordo con gli schemi di correlazione interspecifica e possono rinforzare la risposta alla selezione imposta dal riscaldamento globale.

### INTRODUCTION

Migration in birds involves a number of physiological, morphological, behavioural and life history adaptations to cover the migratory journey and to organise the different annual activities, i.e. breeding, moult, and migration (see, for instance, Berthold 1993, Dingle 1996). Most of these adaptations are not distributed in an all-or-none fashion among migratory and nonmigratory birds, but show considerable variation within and among avian populations. Weismann (1878) already remarked that within one species we may find a graded series of different migratory habits, from completely sedentary to distinctly migratory (cf. Lack 1968). He further outlined how migration may have evolved by gradually increasing the distance and regularity of migratory movements (cf. Terrill 1990). Moreover, the expres-

sion of migratory traits is not independent from one another, as many traits covary within and among populations. In among-species comparisons in the wild and under experimental conditions in the lab, it has been found that birds migrating short or middle distances migrate later than long-distance migrants (cf. Berthold 1990 & 1993). This suggests that the timing of the onset of autumn migration and the migration distance are negatively correlated, i.e. the longer the migration distance the earlier a bird species leaves the breeding grounds. Moreover, migratory activity in long-distance migrants lasts longer and is more intensive than in short-distance migrants (Berthold 1988, Gwinner 1996). In partially migratory bird species, migration distances in the migratory fraction of the population are lower than in species where apparently all individuals migrate. This relation was confirmed in a common garden ex-

periment with Blackcaps from populations with different migratory habits: migratory activities in migrants decrease with increasing proportion of migrants in the population (Berthold & Querner 1981). Among-population covariation can have a number of causes, of which genetic correlation, caused by pleiotropy, epistasis, or linkage, is the only mechanism which influences evolutionary trajectories within populations directly and consistently (Armbruster & Schwaegerle 1996).

Since the landmark papers by Lande (1979, 1982), the role of genetic correlations in the evolution of character complexes has gained considerable attention (see reviews by Price & Langen 1992, Arnold 1992, 1994, and chapter 5 in Roff 1997). Genetic correlations among traits may constrain evolution, i.e. selection for a certain combination of traits is prevented or retarded if selection on one trait cancels selection on another trait (see, for instance, Scheiner & Istock 1991, Arnold 1992, Björklund 1996), or may maintain maladaptive traits (Price & Langen 1992). Drawing on morphological data on two flycatcher species, Merilä *et al.* (1994) demonstrated that even relatively low genetic correlations of approximately 0.2 can considerably constrain short-term selection responses in natural populations. Furthermore, Schluter's (1996) analyses of morphological evolution in sticklebacks and other vertebrate species (including data on different bird groups) suggest that genetic covariances may constrain adaptive evolution over fairly long time spans. However, correlations may also increase the rate of adaptive evolution: if genetic correlations are in the direction of the selection vectors, the net selection responses for all traits will be higher and evolutionary change of all correlated characters will be accelerated (reinforcing correlations). It has been predicted on theoretical and empirical grounds that if correlational selection persists over an extended period of time, concurrent genetic correlations may evolve (Cheverud 1984, Jernigan *et al.* 1994, Endler 1995, Armbruster & Schwaegerle 1996). Therefore, the sign and magnitude of genetic correlations may not only provide information on the direction and rate at which suites of traits will evolve, but will also help to identify periods of correlational selection in the past.

Evidence for the genetic integration of migratory traits has been found in a variety of organisms, predominantly insects (Dingle 1996). Integration is measurable as the genetic correlation among traits. In several model systems, for instance the Milkweed Bug and the Sand Cricket, significant genetic correlations among life history, behavioural, physiological or morphological traits involved in the migratory syndrome have been found (Hegmann & Dingle 1982, Palmer & Dingle 1986 & 1989, Fairbairn & Roff 1990). In some of these species, genetic integration of migratory traits could be ascribed to the pervasive influence of juvenile hormone during individual devel-

opment (see, for instance, Zera & Zhang 1995, Fairbairn & Yadlowski 1996, Dingle & Winchell 1997). In birds, however, information on the genetic correlation among migratory traits and their potential causes is still completely lacking.

Here we review published and unpublished preliminary results on the genetic variances and genetic correlations among migratory traits, and discuss them in view of their influence on evolutionary trajectories. The work presented here is part of a comprehensive study on the evolutionary quantitative genetics of migratory behaviour in the Blackcap (Berthold & Pulido 1994, Pulido *et al.* 1996, Pulido 1998, Pulido & Berthold, *unpublished*). The aim of this study is to assess quantitative genetic parameters of diverse migratory traits in the Blackcap in order to predict evolutionary changes in the wild, and to elaborate models of the microevolution of migratory behaviour in birds.

## MATERIALS AND METHODS

For studying the genetic correlation between the incidence and amount of migratory activity we used the data on migratory activities of 775 Blackcaps from the partially migratory population of southern France (see Berthold 1986, Pulido *et al.* 1996). Details of the methods, the analyses and the results are found in Pulido *et al.* (1996) and Pulido (1998). Phenotypic correlations in southern German Blackcaps were estimated using 385 individuals taken as nestlings from the wild, and reared and kept under controlled conditions (for details, see Berthold & Pulido 1994). Heritabilities and genetic correlations were assessed using data on migratory restlessness of 127 F<sub>1</sub>-offspring, and their respective parents (from 30 families). Heritability estimates were obtained by midparent-offspring regression. Genetic correlations were estimated by offspring on midparent correlation across pairs of traits. This approach yielded two different estimates which we used to obtain an overall genetic correlation by calculating the arithmetic and geometric mean (*cf.* Becker 1992, Falconer & Mackay 1996, Roff 1997). The consistency among these estimates was an indicator of the reliability of the overall estimate.

## RESULTS

### Heritabilities

Heritabilities of the amount, the onset and the intensity of migratory activity were all moderate to high (0.45, 0.37, 0.54), and highly significant (see Table 1). The heritability for the termination of migratory activity was low (0.12) and not significantly different from zero (Berthold & Pulido 1994, Pulido 1998, Pulido & Berthold, *in prep.*).

		AMA	OMA	TMA	IMA
Amount of MA	(AMA)	0.45	---	(+++)	+++
Onset of MA	(OMA)	--	0.37	(---)	---
Termination of MA	(TMA)	++	-	(0.12)	(+++)
Intensity of MA	(IMA)	+++	-	(+)	0.54

Table 1 - Heritabilities (on the diagonal), phenotypic correlations (below diagonal) and genetic correlations (above diagonal) between migratory traits (MA = autumn migratory activity). The sign and the approximate magnitude of the correlations are given (+++:  $r > 0.6$ ; ++:  $0.6 \geq r > 0.3$ ; +:  $0.3 \geq r > 0$ ; -:  $0 > r > -0.3$ ; --:  $-0.3 \geq r > -0.6$ ; ---:  $-0.6 \geq r$ ). Brackets indicate heritability estimates and phenotypic correlations not statistically different from zero, or inconsistent genetic correlations.

### Genetic correlations

Both the results from a bi-directional selection experiment for lower and higher proportion of migrants (Figure 1) and a logistic regression analysis of the probability for migratory Blackcaps having nonmigratory offspring (results not shown, see Pulido *et al.* 1996) indicate that there is a high genetic correlation between the incidence and the amount of migratory activity. The estimate of the realised genetic correlation derived from the selection experiment is not significantly different from one (Figure 1).

Table 1 gives preliminary estimates of the phenotypic and genetic correlations among different migratory traits in the southern German Blackcap population. The results reveal three striking features: (1) Genetic and phenotypic correlations are of the same sign; (2) Genetic correlations are very high, and are consistent when estimated by different methods (except correlations with the termination of migration); (3) Genetic and phenotypic correlations are in the direction expected from among-population phenotypic correlations.

## DISCUSSION

### Heritabilities

We found relatively high heritabilities (*cf.* Mousseau & Roff 1987) for all migratory traits except for the termination of autumn activity, suggesting that the evolution of migratory behaviour will not be constrained by the lack of additive genetic variance (see Berthold *et al.* 1990, Berthold & Helbig 1992, Berthold *et al.* 1992). Berthold & Pulido (1994) showed that mean migratory activity in the southern German Blackcap population, a trait with a mean heritability of 0.4, could change considerably after only short periods (< 30 generations) of moderate directional selection. This change in mean activity could either be achieved by changing the duration of migratory activity (by selecting for earlier or later onset), or by changing the intensity of migration. However, parent-offspring resemblances in the termination of migratory activity are low and not significantly different from zero. This result is in accord with a number of other studies showing that under unfavourable conditions the end of activity may be experimentally de-

layed in the lab (see Terrill 1987, Gwinner *et al.* 1988) or in the field (Perdeck 1964, Terrill & Ohmart 1984), indicating the sensitivity of this trait to environmental variation.

### Genetic Correlations

Our preliminary characterisation of the genetic architecture of migratory traits in the Blackcap demonstrates for the first time that migratory traits in birds are tightly linked by genetic correlations, and thus can be expected to evolve in a concerted fashion as a migratory syndrome.

The strong correlated response of migratory activity to selection for lower and higher proportions of migrants in the southern French Blackcap population, yielding a genetic correlation close to one, suggests that both traits are controlled by the same set of genes. This "one-trait hypothesis" is further corroborated by a significant logistic regression of frequency of migrants among the offspring on mid-parental migratory activity, and by the distributions of migratory activities in different cohorts which are best fitted by a censored normal distribution (Pulido *et al.* 1996). Therefore, incidence and amount of mi-

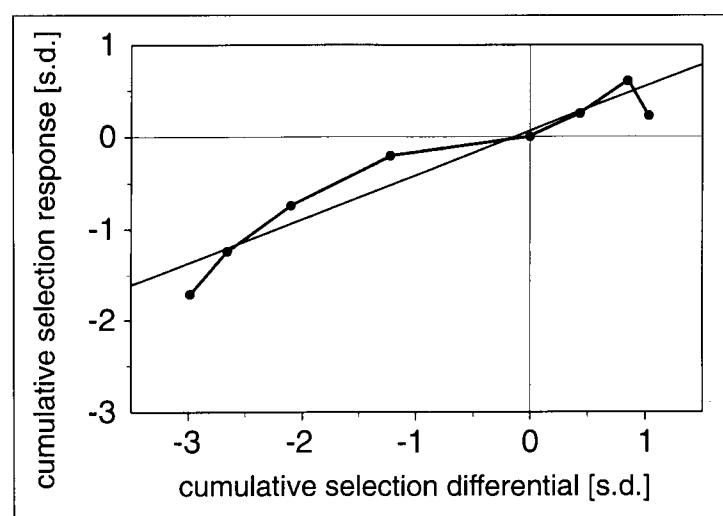


Figure 1 - Correlated response of the amount of migratory activity to selection on the frequency of migrants and nonmigrants. Correlated selection responses (CR) and selection intensities (I) are given in standard deviations of the population mean of the respective parental generation. Points give single-generation cumulative selection responses and intensities. A linear regression line was fitted to all single generation cumulative selection responses and intensities ( $CR = 0.472 I + 0.042$ ). The resultant realised genetic correlation lies between 0.96-1.11. (From Pulido *et al.* 1996).

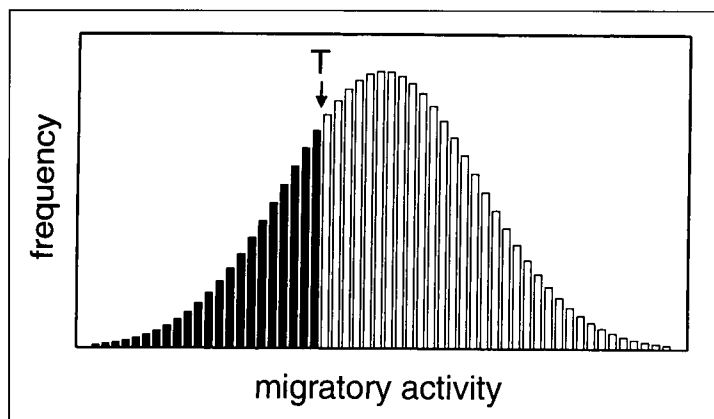


Figure 2 - "One-trait-model" (threshold model) of the relationship between incidence (frequency) and amount of migratory activity. Nonmigrants (in black) are individuals with an (unexpressed) amount of activity below a threshold value (T). (From Pulido *et al.* 1996).

gratory activity should best be viewed as two different aspects of a single trait. Migratory activity is the continuous variable underlying a threshold trait (see Falconer & Mackay 1996, Roff 1996), the incidence of activity. Nonmigratory individuals would thus be those individuals which have activities below a certain threshold value (see Figure 2). The position of the threshold may also be amenable to natural selection (Fairbairn 1994, Fairbairn & Yadlowski 1996, Pulido *et al.* 1996). The frequency of migrants may thus either be changed (1) by directly selecting for or against migrants, (2) by selecting for lower or higher amount of migratory activity in migrants, or (3) by lowering or increasing the threshold for the expression of activity. This genetic "build-up" of migratory activity in the Blackcap has profound implications for the evolution of migration: partial migration should be ubiquitous, and adaptive changes from sedentariness to migratoriness or from migratoriness to residency should be possible by "simply" selecting for shorter or longer migration distances, or by changing the migration threshold, without any need for introducing new genes for "residency" or "migratoriness" (Pulido *et al.* 1996).

The signs of the correlations among migratory traits are in accord with among-species correlations suggesting that they are caused either by develop-

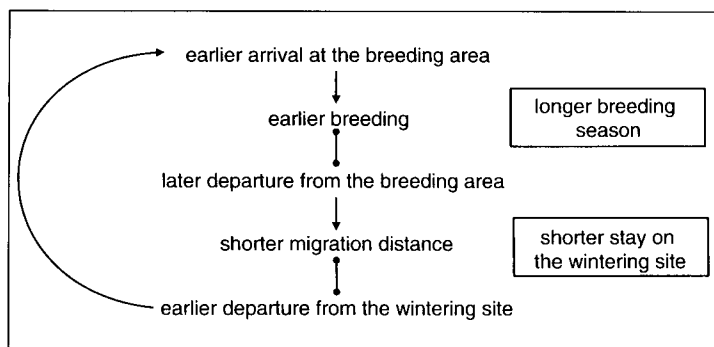


Figure 3 - Expected changes in the timing of breeding and migration of northern Palaearctic birds as a consequence of global warming. Arrows indicate causal links (for instance, earlier departure from the wintering site causes an earlier arrival at the breeding grounds).

mental or physical constraints, or similar selection regimes act on different species in the same way (see, for instance, Sokal 1978, Maynard Smith *et al.* 1985, Armbruster & Schwaegerle 1996). Furthermore, the signs of the correlations match the signs of the multivariate correlational selection caused by global temperature changes (Figure 3). Thus, they will "act" synergistically with this selection regime, reinforcing adaptive changes in all of these traits. Berthold (1991) predicted that "warmer autumn, winter, and spring periods should thus (1) rapidly shift the proportions of obligate partially migratory species towards sedentariness, and (2) individuals of middle to short distance migrants should continuously be selected for shorter migration distances." These selection processes will not operate independently but will reinforce each other, thus increasing the rate of adaptive evolution (correlational selection). We thus expect concerted adaptive responses of migratory traits to selection imposed by global warming. Populations of short and middle distance migrants will very rapidly change their behaviour in response to milder winters by delaying their departure in autumn, by migrating shorter distances (or not at all), and by anticipating their return to the breeding grounds in spring. In long-distance migrants crossing large areas of unsuitable habitat (for instance desert or sea), however, the potential for concerted evolution towards increasing residency (i.e. shorter migration distance and a longer stay on the breeding grounds) is very restricted as a gradual shift of the wintering area towards the breeding grounds is not possible. If, for instance, selection on the breeding ground favours birds departing late in autumn, a shortening of the migration distance will be selected for as a correlated response - this, however, is only possible within the range of suitable overwintering habitats. Selection against migration to unsuitable wintering grounds (for instance deserts) would oppose selection for increased residency. Thus, the same correlation structure which is reinforcing for one population under a specific selection regime can hinder another population from adapting to changing environmental conditions.

Endler (1995) stated that "given enough correlational selection for long enough time, and isolation,..., the pattern of genetic variation and covariation among traits in a population will evolve to 'fit' the local selection and correlational selection network...The net effect will be that traits are genetically, functionally and selectively correlated,...". We believe that this holds for migratory traits in the Blackcap. Throughout their evolutionary history, Palaearctic birds have been exposed to cycles of global warming and cooling. These environmental changes have been, and continue to be accompanied by changes in the winter and summer distribution of bird species (Gauthreaux 1980, Burton 1995), thus moulding avian migratory habits and the genetic correlation structure among traits by natural selection (*cf.* Dingle 1996).

We thus expect genetic correlations to have significant influence on evolutionary trajectories of migratory behaviour. They may either slow down or increase selection responses, depending on the extant multivariate fitness landscapes. In the Blackcap, selection for decreased migratoriness, currently favoured by a temperature rise in the Western Palaearctic, should be reinforced by the genetic architecture of migratory traits. However, in some populations (for instance in the northern and eastern part of the range; cf. Klein *et al.* 1973) unfavourable geographic distribution of wintering areas may prevent adaptive evolution.

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### REFERENCES

- ARMBRUSTER W. S. & SCHWAEGERLE K. E., 1996 - Causes of covariation of phenotypic traits among populations. *J. Evol. Biol.*, 9: 261-276.
- ARNOLD S. J., 1992 - Constraints on phenotypic evolution. *Am. Nat.*, 140 (Suppl.): S85-S107.
- ARNOLD S. J., 1994 - Multivariate inheritance and evolution: a review of concepts. In: Boake C. R. B. (ed.), *Quantitative Genetic Studies of Behavioral Evolution*: 17-48. University of Chicago Press, Chicago.
- BECKER W. A., 1992 - Manual of quantitative genetics. 5th Ed. Academic Enterprises, Pullman, Washington.
- BERTHOLD P., 1986 - Wintering in a partially migratory Mediterranean Blackcap (*Sylvia atricapilla*) population: strategy, control, and unanswered questions. *Ric. Biol. Selvaggina* (Suppl., 10): 33-45.
- BERTHOLD P., 1988 - The control of migration in European warblers. *Acta XIX Congr. Intern. Ornithol.*: 215-249.
- BERTHOLD P., 1990 - Wegzugbeginn und Einsetzen der Zugunruhe bei 19 Vogelpopulationen - eine vergleichende Untersuchung. Proc. Int. 100. DO-G Meeting, Current Topics Avian Biol., Bonn 1988: 217-222.
- BERTHOLD P., 1991 - Patterns of avian migration in light of current global "greenhouse" effects: a central European perspective. *Acta XX Congr. Intern. Ornithol.*: 780-786.
- BERTHOLD P., 1993 - Bird migration: a general survey. Oxford University Press, Oxford.
- BERTHOLD P., 1996 - Control of bird migration. Chapman & Hall, London.
- BERTHOLD P. & HELBIG A. J., 1992 - The genetics of bird migration: stimulus, timing, and direction. *Ibis*, 134 (Suppl. 1): 35-40.
- BERTHOLD P., HELBIG A. J., MOHR G. & QUERNER U., 1992 - Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, 360: 668-670.
- BERTHOLD P., MOHR G. & QUERNER U., 1990 - Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilziehverhaltens: Ergebnisse eines Zweiweg-Selektionsexperiments mit der Mönchsgrasmücke (*Sylvia atricapilla*). *J. Orn.*, 131: 33-45.
- BERTHOLD P. & PULIDO F., 1994 - Heritability of migratory activity in a natural bird population. *Proc. R. Soc. Lond. B*, 257: 311-315.
- BERTHOLD P. & QUERNER U., 1981 - Genetic basis of migratory behavior in European warblers. *Science*, 212: 77-79.
- BJÖRKLUND M., 1996 - The importance of evolutionary constraints in ecological time scales. *Evol. Ecol.*, 10: 423-431.
- BURTON J. F., 1995 - Birds and climate change. Christopher Helm, London.
- CHEVERUD J. M., 1984 - Quantitative genetics and developmental constraints on evolution by selection. *J. Theor. Biol.*, 110: 155-171.
- DINGLE H., 1996 - Migration: the biology of life on the move. Oxford University Press, New York.
- DINGLE H. & WINCHELL R., 1997 - Juvenile hormone as a mediator of plasticity in insect life. *Arch. Insect Biochem. Physiol.*, 35: 359-373.
- ENDLER J. A., 1995 - Multiple-trait coevolution and environmental gradients in guppies. *Trends Ecol. Evol.*, 10: 22-29.
- FAIRBAIRN D. J., 1994 - Wing dimorphism and the migratory syndrome: correlated traits for migratory tendency in wing dimorphic insects. *Res. Popul. Ecol.*, 36: 157-163.
- FAIRBAIRN D. J. & ROFF D. A., 1990 - Genetic correlations among traits determining migratory tendency in the Sand Cricket, *Gryllus firmus*. *Evolution*, 44: 1787-1795.
- FAIRBAIRN D. J. & YADLOWSKI D. E., 1996 - Coevolution of traits determining migratory tendency: correlated response of a critical enzyme, juvenile hormone esterase, to selection on wing morphology. *J. Evol. Biol.*, 10: 495-513.
- FALCONER D. S. & MACKAY T. F. C., 1996 - Introduction to quantitative genetics. 4th Ed. Longman, Harlow.
- GAUTHREAUX S. A., 1980 - The influences of long-term and short-term climatic changes on the dispersal and migration of organisms. In: Gauthreaux S. A. (ed.), *Animal migration, orientation, and navigation*: 103-174. Academic Press, New York.
- GWINNER E., 1996 - Circannual clocks in avian reproduction and migration. *Ibis*, 138: 47-63.
- GWINNER E., SCHWABL H. & SCHWABL-BENZINGER I., 1988 - Effects of food-deprivation on migratory restlessness and diurnal activity in the Garden Warbler *Sylvia borin*. *Oecologia*, 77: 321-326.
- HEGMANN J. P. & DINGLE H., 1982 - Phenotypic and genetic covariance structure in Milkweed Bugs (*Oncopeltus fasciatus*). In: Dingle, H. & Hegmann, J. P. (eds.), *Evolution and genetics of life histories*: 177-185. Springer-Verlag, New York.
- JERNIGAN R. W., CULVER D. C. & FONG D. W., 1994 - The dual role of selection and evolutionary history as reflected in genetic correlations. *Evolution*, 48: 587-596.
- KLEIN H., BERTHOLD P. & GWINNER E., 1973 - Der Zug europäischer Garten- und Mönchsgrasmücken (*Sylvia borin* und *S. atricapilla*). *Vogelwarte*, 27: 73-134.
- LACK D., 1968 - Bird migration and natural selection. *Oikos*, 19: 1-9.
- LANDE R., 1979 - Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution*, 33: 402-416.
- LANDE R., 1982 - A quantitative genetic theory of life history evolution. *Ecology*, 63: 607-615.
- MAYNARD SMITH J., BURIAN R., KAUFFMAN S., ALBERCH P., CAMPBELL J., GOODWIN B., LANDE R., RAUP D. & WOLPERT L., 1985 - Developmental constraints and evolution. *Quart. Rev. Biol.*, 60: 265-287.
- MERILÄ J., BJÖRKLUND M. & GUSTAFSON L., 1994 - Evolution

- of morphological differences with moderate genetic correlations among traits as exemplified by two flycatcher species (*Ficedula*; Muscipidae). *Biol. J. Linn. Soc.*, 52: 19-30.
- MOUSSEAU T. A. & ROFF D. A., 1987 - Natural selection and the heritability of fitness components. *Heredity*, 59: 181-197.
- PALMER J. O. & DINGLE H., 1986 - Direct and correlated responses to selection among life-history traits in Milkweed Bugs (*Oncopeltus fasciatus*). *Evolution*, 40: 767-777.
- PALMER J. O. & DINGLE H., 1989 - Responses to selection on flight behavior in a migratory population of Milkweed Bug (*Oncopeltus fasciatus*). *Evolution*, 43: 1805-1808.
- PERDECK A. C., 1964 - An experiment on the ending of autumn migration in Starlings. *Ardea*, 52: 133-139.
- PRICE T. & LANGEN T., 1992 - The evolution of correlated characters. *Trends Ecol. Evol.*, 7: 307-310.
- PULIDO F., 1998 - Evolutionary quantitative genetics of migratory restlessness in the Blackcap (*Sylvia atricapilla*). Ph.D. thesis, University of Constance.
- PULIDO F., BERTHOLD P. & VAN NOORDWIJK A. J., 1996 - Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. *Proc. Natl. Acad. Sci. USA*, 93: 14642-14647.
- ROFF D. A., 1996 - The evolution of threshold traits in animals. *Quart. Rev. Biol.*, 71: 3-35.
- ROFF D. A., 1997 - Evolutionary quantitative genetics. Chapman & Hall, New York.
- SCHEINER S. M. & ISTOCK C. A., 1991 - Correlational selection on life history traits in the Pitcher Plant Mosquito. *Genetica*, 84: 123-128.
- SCHLUTER D., 1996 - Adaptive radiation along genetic lines of least resistance. *Evolution*, 50: 1766-1774.
- SOKAL R. R., 1978 - Population differentiation: something new or more of the same. In: Brussard, F. (ed.), *Ecological genetics: the interface*: 215-239. Springer-Verlag, New York.
- TERRILL S. B., 1987 - Social dominance and migratory restlessness in the Dark-eyed Junco (*Junco hyemalis*). *Behav. Ecol. Sociobiol.*, 21: 1-11.
- TERRILL S. B., 1990 - Evolutionary aspects of orientation and migration in birds. *Experientia*, 46: 395-404.
- TERRILL S. B. & OHMART R. D., 1984 - Facultative extension of fall migration by Yellow-rumped Warblers (*Dendroica coronata*). *Auk*, 101: 427-438.
- WEISMANN A., 1878 - Ueber das Wandern der Vögel. Carl Habel Verlag, Berlin.
- Zera A. J. & Zhang C., 1995 - Evolutionary endocrinology of juvenile hormone esterase in *Gryllus assimilis*: direct and correlated responses to selection. *Genetics*, 141: 1125-1134.