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Life history traits of Palaearctic and Nearctic migrant passerines

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I studied the life history consequences of tropical migration in passerine birds from Europe, and eastern and western North America. Tropical migrants were compared with more sedentary birds within a region. Analyses were conducted at two different taxonomic levels. First, at the generic level, I investigated whether there was any difference between migratory habit groups in general. If a genus consisted of species with different migratory habits, these were treated separately. Second, analysis at the within-family level (between-family differences eliminated) was used to assess the role of phylogeny in relation to life history differences observed at the generic level. I also examined the effect of body weight on life history features, using regression.

Features common to tropical migrants on both continents were lower body weight and a smaller number of broods than in more sedentary birds. For a given body weight, tropical migrants also laid smaller clutches than more sedentary birds, but this difference was accounted for by between-family differences and did not indicate a linkage with migration *per se*. Mean annual survivorship did not differ between tropical migrants and more sedentary birds in Europe, whereas eastern Nearctic tropical migrants had a significantly higher survival rate at the within-family level, which may therefore be a direct consequence of wintering in the tropics. In the Nearctics, migratory habit seemed to be a more important factor, affecting other life history features than in Europe, where body weight explained between-genera differences better. The implications of the between-continent differences for conservation are briefly discussed.

1. Introduction

The existence of migratory birds in different bird families in geographically widely separated areas suggests that avian migration has evolved independently many times. It has been proposed that the migratory habit is a basic strategy affecting many other life history and ecological attributes of birds (Fretwell 1972, Mönkkönen & Helle 1987).

Avian life history strategies have been studied intensively. For example, the relationship between body size and life history strategy is particularly well known (Linstedt & Calder 1976, Western & Ssemakula 1982, Zammuto 1986, Sæther 1987, 1989, Dobson 1990). In addition, the trade-off between reproductive effort and survival rate in a species has been demonstrated by a number of workers (Ekman & Askenmo 1986, Zammuto 1986, Sæther 1988, Dobson

1990, but see Lindén & Møller 1989). Attention has also focused on the life history correlates of habitat (Southwood 1977, 1988) and migratory habit (Herrera 1978, Whitcomb et al. 1981, O'Connor 1981, Dobson 1990), but comparative studies are lacking.

Traditionally, migrants were regarded as fugitive species that use sporadic, superabundant resources, and conventionally speaking, they are more r-selected than sedentary birds (Karr 1976, O'Connor 1981). This view, however, has been challenged by studies from the Nearctic (Whitcomb et al. 1981), Neotropical (Rappole et al. 1983) and Palaeotropical regions (Rabøl 1987), which show that migrants function as integral members of the communities that they inhabit. In this paper, I compare the life history traits of Palaearctic and Nearctic tropical migrants with those of more sedentary birds. Resident and short-distance migrant birds from different parts of the Holarctic region are more closely related to each other than are tropical migrants, thus providing a comparison with which to evaluate the consequences of long-distance migration (Helle & Mönkkönen 1990, Mönkkönen et al. 1992). I also assess the role of phylogeny in relation to life history attributes.

2. Concepts and definitions

This study focuses only on passerine birds breeding regularly in Europe and North America (north of the U.S.-Mexican border). Introduced species and Palaearctic species breeding only in the Aleutians and/or Western Alaska were not considered to belong to the New World avifauna. As I wanted to concentrate on temperate bird species, I also excluded some tropical species from the New World data, because their ranges only slightly overlapped southern Texas or Florida. For species lists I consulted Bruun and Singer (1971) and Scott et al. (1987) for Europe and North America, respectively. Species were categorized according to their migratory habit using the distribution maps in these field-guides. A species was defined as a tropical migrant if its wintering area was completely south of the Sahara (for Palaeartic migrants) or south of the United States (for Nearctic migrants). Residents and short-distance migrants were not separated, as the distinction between them varies according to latitude.

As previous studies suggested that there were differences in the habitat associations of migrant bird species from eastern and western North America (Rosenberg & Raphael 1987, Mönkkönen & Helle 1989, Mönkkönen et al. 1992), I treated these two regions separately. Furthermore, western and eastern North American migrants have largely non-overlapping wintering quarters (Hutto 1985, Terborgh 1989). Longitude 105°W was selected as the border between eastern and western parts. Naturally, some species are included in both eastern and western data sets. In this paper, I follow the classification provided by Sibley et al. (1988).

3. Material and methods

Information on clutch size and number of broods per breeding season was obtained from Harrison (1975) for Palaearctic and from Ehrlich et al. (1988) for Nearctic species. If these sources reported a range of clutch size and brood number, I used the average for each parameter. The number of eggs produced by an average female per breeding season was calculated by multiplying clutch size by brood number. The above-mentioned books were also consulted for information on nest location.

I used records of maximum longevity (Rydzewski 1978, 1979, Clapp et al. 1983, Klimkiewicz et al. 1983, Klimkiewicz & Futcher 1987, Saurola 1988) to estimate the life-spans of the bird species (see Whitcomb et al. 1981). The annual survivorship of adult birds was preferably calculated from ringing recoveries, as in Lack (1950) and Haldane (1955), but in the absence of recovery data, it was also estimated from the return rates of individually marked birds. Since the return rate obviously underestimates survivorship (e.g. Frankhauser 1971), due to factors such as incomplete site fidelity, return rate values were corrected by multiplying them by the average ratio of survival to return rate. This coefficient was calculated using information only from species for which both return and survival rate estimates were available. Survival rates and their sources are listed in the Appendix.

Species-specific weights were obtained from Stewart (1937), von Haartman et al. (1963–72), Holmes & Sturges (1975), Järvinen & Väisänen (1977a), Clench & Leberman (1978), Blondel et al. (1984), Speirs (1985), Murphy (1989), and Kulesza (1990). As reproductive traits of birds have been shown to be allometrically scaled with body size (Sæther 1985, 1987, Zammuto 1986), weight was used to check for the effect of body size (see below).

I analysed the data at the generic and within-family level. First, I compared tropical migrant and other passerine genera using the average of species-specific values for each trait (mode for nest location). If a genus consisted of species with different migratory strategies, these were treated separately. At this level (called generic level, hereafter), I was interested to discover whether there was any difference between migratory habit groups in general. Second, I eliminated between-family differences by standardizing the data so that for each family and trait the mean was set to zero and standard deviation to unity (PROC STANDARD, SAS Institute Inc. 1988). I conducted subsequent analyses to detect patterns across genera within families, contrasting tropical migrants with other genera (called within-family level, hereafter) to determine whether differences were associated with the migratory pattern within families or whether they were due to between-family differences. This may guide us in investigating the origin of possible differences. If the difference stems from the within-family level, the reasons are likely to be of more recent origin, reflecting pressures caused by migrancy, *per se*; differences emerging only at the between-family level (i.e. at the generic level but not at the within-family level) indicate greater importance of historical factors. Sæther (1987, 1989) concluded that much of the variation in avian life histories is due to their early evolutionary history, having little bearing on contemporary conditions. He further recommended that "any study of the adaptive significance of life history variation in birds must consider the effect of phylogeny" (Sæther 1989, see also Murphy 1989).

The effect of body size was eliminated using regression. First, a linear regression was performed between log-transformed weight and each of the life history traits. If body weight significantly explained the variation in a given trait, the residual values were used to detect whether the migratory habit groups differed for a given body weight. I tested the differences between tropical migrants and more sedentary birds using the Mann-Whitney U-test (z-conversion). In interpreting the results, attention was also paid to biologically interesting trends, and therefore a difference at a probability level of 0.1 was considered important.

4. Results

In both North America and Europe, tropical migrant passerines weighed less than bird genera with other migratory strategies (Table 1). A similar trend was also observed within families, although the difference was significant only in eastern North America. These results suggested advisability of considering the effect of allometry on other traits.

Table 1. Average weight of tropical migrant passerine genera (TRM) compared to that of more sedentary birds (Other) at two levels of analysis. Generic level refers to values averaged across families, whereas within-family level gives indices after the between-family differences were removed (mean for each family set to zero, and standard deviation to unity).

		Western North America			Eastern North America			Europe		
Level		n	mean	P	n	mean	P	n	mean	P
Generic	TRM	24	23.0	0.077	29	23.3	0.095	20	20.5	0.021
	Other	61	46.7		55	44.7		39	58.9	
Within-family	TRM	24	–0.28	0.138	29	–0.20	0.037	20	–0.21	0.102
	Other	61	0.11		55	0.15		39	0.11	

Migratory habit appeared to have only a minor effect on nest location in passerine bird genera; the distribution of genera into nest location classes did not differ between tropical migrants and other passerines in any of the regions considered here (Table 2). In all areas, however, tropical migrants tend to prefer shrubs as their nest place more than expected.

For a given body weight, tropical migrants lay smaller clutches than other bird genera in all regions (Table 3). In western North America, however, this difference is at least partially accounted for by larger clutch size in hole-nesting species: when the hole nesters were omitted, no statistically significant difference was found, but the trend remained (tropical migrants: residual = –0.23, n = 22; other passerines: residual = 0.09, n = 54; P = 0.186). In other areas the significant difference persisted even when hole nesters were omitted. At the within-family level no significant difference existed.

The number of broods reared per breeding season was significantly lower in tropical migrants than in other birds in eastern and western North America (Table 4). Body weight accounted for the variation in brood number only in Europe, and after allometric scaling, the number of broods in tropical migrants was significantly lower than in other passerines also in Europe. Within families, a lower brood number in tropical migrants was prominent in all areas, and this was not related to body size.

Not surprisingly, the number of eggs laid by a female per breeding season (i.e. clutch size × brood number) was significantly higher in more sedentary birds in all areas at both the generic and within-family level (Table 5).

The record of maximum longevity was highly significantly correlated with body weight in all areas at both the generic and within-family level. When the residual values were compared after checking for body weight, the differences were far from being statistically significant in all areas (Table 6).

In Europe the mean overwinter survival rate of tropical migrants was lower than that of birds with alternative migratory habits. In North America the trends were the opposite, but non-significant (Table 7). Body weight significantly accounted for the difference in survivorship between genera in Europe, and for a given body weight there was no difference between migratory habit groups. Within families, Palaearctic tropical migrants survived as well as birds with alternative migratory habits. Eastern North American tropical migrants had a significantly higher survival rate than other passerines. This trend also existed in western birds, but was not significant (Table 7).

5. Discussion

The relationship between life history strategies and migratory habit is more complex than was thought (Fretwell 1972, O'Connor 1981). Features common to Palaearctic and Nearctic tropical migrants, as compared to more sedentary birds were smaller size, smaller clutch size and lower brood number. Differences could be found in survival rates. Western North American migrant passerines seemed in many features to be intermediate between those of European and eastern North American migrants.

According to this study, eastern North American tropical migrants had a higher overwintering survival rate than more sedentary birds within families. This suggests that phylogenetic factors are not involved, but survival rate is higher as a consequence of wintering in the tropics. The survival rate of European tropical migrants was equal to that of other birds for a given body weight, supporting O'Connor's (1981) findings.

Many studies have shown that tropical migrants have a lower reproductive effort than more sedentary birds (Kipp 1943, Robbins 1979, Greenberg 1980, O'Connor 1981, Whitcomb et al. 1981, Mönkkönen & Helle 1987). In this study, clutch size differed only at the generic level, indicating that tropical migrants evolved predominantly in families with small clutches, and there need not necessarily be any causal link with migration *per se*. By contrast, the lower number of broods in tropical migrants is more likely a general characteristic related to long-distance migration, since this difference is significant at the within-family level. Short-distance migrants have been shown to be multiple-brooded (Mönkkönen & Helle 1987). The European situation, that brood number differed only within

Table 2. Observed (and expected) numbers of genera categorized by nest site location in the three regions. The mode of species-specific attributes was used to classify a genus.

	Nest site					
	Ground	Shrub	Tree	Hole	Other	Total
Eastern North America						
Tropical migrants	6 (8.6)	8 (5.9)	10 (9.0)	3 (3.5)	2 (2.1)	29
Others	19 (16.4)	9 (11.1)	16 (17.0)	7 (6.6)	4 (3.9)	55
Western North America						
Tropical migrants	7 (7.0)	7 (5.9)	8 (8.7)	3 (2.5)	2 (2.8)	27
Others	18 (18.0)	14 (15.1)	23 (22.2)	6 (6.5)	8 (7.2)	69
Europe						
Tropical migrants	7 (6.8)	6 (5.3)	2 (5.0)	3 (2.7)	6 (4.2)	24
Others	16 (16.2)	12 (12.7)	15 (12.0)	6 (6.3)	8 (9.9)	57

Table 3. Average clutch size of tropical migrant passerine genera (TRM) compared to that of more sedentary birds (Other) at two levels of analysis (see Table 1). Residuals denote values for a given body weight after eliminating the effect of weight by regression analysis.

		Western North America			Eastern North America			Europe		
Level		n	mean	P	n	mean	P	n	mean	P
Generic	TRM	27	4.07	0.244	29	4.11	0.109	24	4.85	0.666
	Other	68	4.41		54	4.49		57	5.12	
Residuals	TRM	24	–0.33	0.057	29	–0.31	0.021	20	–0.45	0.031
	Other	60	0.13		54	0.17		42	0.23	
Within-family	TRM	27	–0.11	0.264	29	–0.12	0.288	24	–0.08	0.609
	Others	68	0.04		54	0.07		57	0.03	

Table 4. Average number of broods per breeding season of tropical migrant passerine genera (TRM) compared to that of more sedentary birds (Other) at two levels of analysis (see Table 1). Residuals denote values for a given body weight after the effect of weight was eliminated by regression analysis. Residual values are given only if the regression analysis showed a significant relationship between brood number and body weight.

		Western North America			Eastern North America			Europe		
Level		n	mean	P	n	mean	P	n	mean	P
Generic	TRM	22	1.31	0.002	29	1.27	0.000	24	1.39	0.133
	Other	66	1.66		52	1.69		57	1.61	
Residuals	TRM							20	–0.15	0.091
	Other							39	0.08	
Within-family	TRM	22	–0.39	0.012	29	–0.45	0.000	24	–0.42	0.004
	Others	66	0.13		52	0.25		57	0.18	

Table 5. Average number of eggs laid per breeding season by females of tropical migrant passerine genera (TRM) compared to that of more sedentary birds (Other) at two levels of analysis (see Table 1). Residuals denote values for a given body weight after the effect of weight was eliminated by regression analysis. Residual values are given only if the regression analysis showed a significant relationship between the number of eggs and body weight.

		Western North America			Eastern North America			Europe		
Level		n	mean	P	n	mean	P	n	mean	P
Generic	TRM	22	5.31	0.001	29	5.10	0.000	24	6.73	0.042
	Other	66	7.18		52	7.42		57	8.13	
Residuals	TRM							20	–1.31	0.002
	Other							39	0.67	
Within-family	TRM	22	–0.41	0.010	29	–0.52	0.000	24	–0.41	0.005
	Others	66	0.14		52	0.29		57	0.17	

Table 6. Average maximal life-spans (in months) of tropical migrant passerine genera (TRM) compared to those of more sedentary birds (Other) at two levels of analysis (see Table 1). Residuals denote values for a given body weight after the effect of weight was eliminated by regression analysis. Residual values are given only if the regression analysis showed a significant relationship between maximal life-spans and body weight.

		Western North America			Eastern North America			Europe		
Level		n	mean	P	n	mean	P	n	mean	P
Generic	TRM	24	88.3	0.119	29	97.6	0.103	20	102.3	0.077
	Other	60	104.4		53	113.4		36	121.2	
Residuals	TRM	23	–5.58	0.278	29	–3.73	0.594	19	–1.90	0.582
	Other	54	2.38		53	2.04		33	1.10	
Within-family	TRM	24	–0.19	0.347	29	–0.29	0.023	20	–0.26	0.114
	Other	60	0.08		53	0.16		36	0.14	
Residuals	TRM	23	–0.08	0.529	29	–0.14	0.151			
	Other	54	0.03		53	0.08				

Table 7. Average survival rates of tropical migrant passerine genera (TRM) compared to that of more sedentary birds (Other) at two levels of analysis (see Table 1). Residuals denote values for a given body weight after the effect of weight was eliminated by regression analysis. Residual values are given only if the regression analysis showed a significant relationship between survival and body weight.

		Western North America			Eastern North America			Europe		
Level		n	mean	P	n	mean	P	n	mean	P
Generic	TRM	8	0.56	0.317	12	0.57	0.230	12	0.41	0.003
	Other	18	0.49		23	0.49		27	0.50	
Residuals	TRM							12	–0.03	0.113
	Other							26	0.02	
Within-family	TRM	8	0.38	0.520	12	0.43	0.082	12	–0.24	0.234
	Other	18	–0.17		23	–0.28		27	0.11	

families, clearly suggests a direct consequence of tropical migration.

Whitcomb et al. (1981) found that tropical migrants have significantly longer life-spans for a given body weight than short-distance migrants and residents (measured by the records of maximum longevity). In this study no statistically significant difference was found between migratory strategies. Moreover, the trends were the opposite to that reported by Whitcomb et al. (1981). Obviously, the records of maximum longevity are extremes of very skewed probability distributions and sensitive to differences in sample size, and therefore, not very useful in comparing species with unequal numbers of recoveries.

According to Southwood (1976), an animal's body size is a key factor affecting other life history features (see also Peters 1983). Previous studies have shown that tropical migrants are smaller than residents and short-distance migrants (O'Connor 1981, Whitcomb et al. 1981, Leisler 1990). The results obtained here corroborate these findings. Moreover, the North American data suggested that migratory habit as such is important with respect to body size, since the tropical migrants are smaller even within families.

No relationship was found between body size and survival rate in North American passerines, although this is evident in birds in general (Sæther 1989). This is presumably partly due to the small variation in size among those species for which I have an estimate of survivorship (from 9 to 120 g). On the other hand, some small migrant species have prominently high survival rates (see e.g. Greenberg 1980, Morse 1989), overriding the general dependence of survival rate on body size. Body size did not correlate either with the number of broods or egg production in North America. Therefore, migratory habit is probably a more important factor than body size in determining other life history strategies in the New World passerines.

Naturally, life history traits are not independent of each other. A high survival rate and low reproductive output — as in the eastern North American migrants in this study — have been shown to be strongly linked (see Introduction). The preference of many eastern North American migrants for temporally stable habitats (mature deciduous forests, see e.g Mönkkönen & Helle 1989) and their high survival rate are also possibly intercorrelated; fast changing early successional habitats are too 'ephemeral' for them.

Life history features can best be understood against the evolutionary history of each species, and it is this background which makes their interrelationships ecologically relevant. The differences between Palaearctic and Nearctic migrant passerines found here in life history features and earlier in habitat association patterns (Mönkkönen and Helle 1989, Mönkkönen et al. 1992) can be traced back to the independent origin and partly different history of migratory birds. The basic difference is that most Nearctic tropical migrants evolved from historically tropical species, whereas Palaearctic migrants are evidently of Palaearctic origin (see Mönkkönen et al. 1992).

In eastern North America, some tropical migrant song bird populations have experienced drastic declines in areas where their breeding habitats have been heavily fragmented (Askins et al. 1990), whereas in Europe migrants have done well in man-made landscapes (e.g. Opdam et al. 1985, Haila 1986). In Europe, it is the resident species of the taiga zone which have suffered the most (Järvinen & Väisänen 1977b, Helle & Järvinen 1986, Virkkala 1990). Due to their history, Palaearctic migrants have life histories more easily adaptable to new situations in altered environments than Nearctic migrants (Mönkkönen et al. 1992). No single life history feature makes a species particularly vulnerable to habitat alterations, rather it is a combination of traits. We cannot change the avian life histories, but our common responsibility is to provide sufficient habitats in breeding, migration and wintering areas, so that viable populations can be maintained even by species with vulnerable combinations of life history attributes.

I have here compared tropical migrants with temperate zone residents; it would be extremely interesting to compare tropical migrants with tropical residents. This would greatly advance our knowledge of the evolution and ecological correlates of migration. General trends and differences reported here could be tested using more specific data from bird genera containing species with different migratory habits.

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Selostus: **Eurooppalaisten ja pohjoisamerikkalaisten varpuslintujen muuttotapa ja elinkierto**

Tutkin kirjallisuudesta kerätyn aineiston perusteella, millaisia elinkierron ominaisuuksia (pesyekoko yms.) liittyy talvehtimiseen tropiikissa Euroopan, sekä itäisen ja läntisen Pohjois-Amerikan varpuslinnuilla. Vertasin näitä pitkän matkan muuttajia kunkin alueen paikkalintuihin ja lyhyen matkan muuttajiin. Analysoin aineiston kahdella taksonomisella tasolla. Vertasin ensin tropiikkiin muuttavia lintusukuja paikallisempiin sukuihin. Jos jossain suvussa oli sekä troopiikkiin muuttavia että muita lajeja, käsittelin näitä erillään. Sukujen välillä havaittavat erot voivat johtua joko heimojen sisäisistä tai välisistä eroista. Tämän takia poistin analyysin toisessa vaiheessa heimojen väliset erot standardoimalla aineiston, ja toistin vertailun. Molemmilla tasoilla tarkistin myös, vaikuttaako ruumiin paino elinkierron ominaisuuksiin.

Molemmilla mantereilla tropiikkiin muuttajat olivat kevyempiä ja munivat vähemmän pesyeitä pesimäkautta kohti kuin paikallisemmat varpuslinnut. Myös pesyekoko oli trooppisilla muuttolinnuilla pienempi, kun painon vaikutus oli poistettu. Tämä kuitenkin johtui heimojen välisistä eroista, eikä pienellä pesyekoolla ole välttämättä mitään yhteyttä muuttotapaan (so. pieni pesyekoko on ennen muuttotapaa kehittynyt ominaisuus). Keskimääräisessä kuolleisuudessa ei ollut eroja eurooppalaisten pitkän matkan muuttajien ja muiden lintujen välillä. Itäisen Pohjois-Amerikan muuttolinnut sen sijaan selvisivät talvesta paremmin kuin muut varpuslinnut, kun vertailu tehtiin aineistolla, josta heimojen väliset erot oli poistettu. Tulos viittaa siihen, että alhainen kuolleisuus on suoranainen seuraus talvehtimisesta tropiikissa. Uudella Mantereella muuttotapa näyttäisi olevan määräävämpi tekijä suhteessa muihin elinkierron ominaisuuksiin kuin Euroopassa, missä paino selittää paremmin sukujen välisiä eroja.

Tropiikkiin muuttavien varpuslintujen kannat ovat taantuneet monin paikoin itäisen Pohjois-Amerikan lehtimetsävyöhykkeellä ihmistoiminnan vaikutuksesta. Euroopan ja läntisen Pohjois-Amerikan muuttolintupopulaatiot sitävastoin ovat säilyneet jotakuinkin entisellä tasollaan tai lisääntyneet viimeisen 50 vuoden aikana. Nämä erot ovat yhteydessä lintulajistojen evolutiiviseen historiaan, joka vaikuttaa niiden kykyyn sopeutua uusiin ympäristöihin ja heijastuu nykyään havaittaviin ekologisiin ja elinkierron ominaisuuksiin. Muuttolintujen suojelu on korostuneesti kansainvälinen tehtävä.

References

Askins, R. A., Lynch, J. F. & Greenberg, R. 1990: Population declines in migratory birds in eastern North America. — In: Power, D. M. (ed.), Curr. Ornithol. 7:1–57.

Baker, M. C., Mewaldt, L. R. & Stewart, R. M. 1981: Demography of White-crowned Sparrows (Zonotrichia leucophrys nuttalli). — Ecology 62:636–644.

Bedard, J. & LaPointe, G. 1984: Banding returns, arrival times, and site fidelity in the Savannah Sparrow. — Wilson Bull. 96:196–205.

Best, L. & Rodenhouse, N. L. 1984: Territory preference of Vesper Sparrows in cropland. — Wilson Bill. 96:72–82.

Blancher, P. J. & Robertson, R. J. 1985: Site consistency in Kingbird breeding performance: implications for site fidelity. — J. Anim. Ecol. 54:1017–1027.

Blondel, J., Vuilleumier, F., Marcus, L. F. & Terouanne, E. 1984: Is there ecomorphological convergence among Mediterranean bird communities of Chile, California, and France? — In: Hecht, M. K., Wallace, B. & Prance, G. T. (eds.), Evolutionary Biology 18:141–213.

Bruun, B. & Singer, A. 1971: The Hamlyn guide to birds of Britain and Europe. — Hamlyn Publisher Group Ltd, Feltham. 320 pp.

Clapp, R. B., Klimkiewicz, M. K. & Futcher, A. G. 1983: Longevity records of North American birds: Columbidae through Paridae. — J. Field Ornithol. 54:123–137.

Clench, M. H. & Leberman, R. C. 1978: Weights of 151 species of Pennsylvania birds analysed by month, age, and sex. — Bull. Carnegie Mus. Nat. Hist. 5:1–85.

Coulson, J. C. 1960: A study of mortality of the Starling based on ringing recoveries. — J. Anim. Ecol. 29:251–271.

Czarnecki Z. 1975: Studies concerning banded bird populations nesting in riverside willows. (In Polish with English summary) — Acta Ornithol. 15:1–79.

Darley, J. A., Scott, D. M. & Taylor, N. K. 1977: Effects of age, sex and breeding success on site fidelity of Gray Catbirds. — Bird-Banding 48:145–151.

Dobson, A. P. 1990: Survival rates and their relationship to life-history traits in some common British birds. — In: Power, D. M. (ed.), Curr. Ornithol. 7:115–146.

Drilling, N. E. & Thompson, C. F. 1988: Natal and breeding dispersal in House Wrens (Troglodytes aedon). — Auk 105:480–491.

Ehrlich, P., Dobkin, D. & Wheye, D. 1988: The birders handbook. A field guide to the natural history of North American birds. — Simon & Schuster, N.Y. 785 pp.

Ekman, J. 1984: Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (Parus montanus). — J. Anim. Ecol. 53:119–130.

Ekman, J. & Askenmo, C. 1986: Reproductive cost, age-specific survival and a comparison of the reproductive strategy in two European tits (Genus Parus). — Evolution 40:159–168.

Elder, W. H. 1985: Survivorship in the Tufted Titmouse. — Wilson Bull. 97:517–524.

Eliason, B. C. 1986: Female site fidelity and polygyny in the Blackpoll Warbler (Dendroica striata). — Auk 103:782–790.

Farner, D. S. 1955: Bird banding in the study of population dynamics. — In: Wolfson, A. (ed.), Recent studies in avian biology: 397–449. Univ. Illinois Press, Urbana.

Frankhauser, D. P. 1971: Annual adult survival rates in blackbirds and starlings. — Bird-Banding 42:36–42.

Fretwell, S. D. 1972: Populations in a seasonal environment. — Princeton University Press, Princeton. 217 pp.

Gavin, T. A. & Bollinger, E. K. 1988: Reproductive correlates of breeding-site fidelity in Bobolinks (Dolichonyx oryzivorus). — Ecology 69:96–103.

Greenberg, R. 1980: Demographic aspects of long-distance migration. — In: Keast, A. & Morton, E. S. (eds.), Migrant birds in the neotropics: ecology, behaviour, distribution, and conservation: 493–504. Smithsonian Inst. Press, Washington, D.C.

Gustafsson, L. 1985: Fitness factors in the Collared Flycatcher Ficedula albicollis, Temm. — Ph.D. Thesis, Acta Universitatis Uppsaliensis, Uppsala. 38 pp.

Haartman, L. von, Hilden, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin. — Otava, Helsinki.

Haas, C. A. & Sloane, S. A. 1989: Low return rates of migratory Loggerhead Shrikes: winter mortality or low site fidelity? — Wilson Bull. 101:458–460.

Haila, Y. 1986: North European land birds in forest fragments: Evidence for area effects? — In: Verner, J., Morrison, M. & Ralph, C. J. (eds.): Wildlife 2000. Modelling habitat relationships of terrestrial vertebrates: 315–319. Univ. Wisconsin Press, Madison.

Haldane, J. B. S. 1955: The calculation of mortality rates from ringing data. — Acta XI Congr. Int. Ornithol. 1954:454–458.

Harrison, C. 1975: A field guide to the nests, eggs, and nestlings of European birds with North Africa and the Middle East. — William Collins Sons & Co Ltd, Glasgow. 432 pp.

Haukioja, E. 1969: Mortality rates of some Finnish passerines. — Ornis Fennica 46:171–178.

Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — Oikos 46:107–115.

Helle, P. & Mönkkönen, M. 1990: Forest succession and bird communities: theoretical aspects and practical implications. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 299–318. SPB Academic Publishing bv, the Hague.

Herrera, C. M. 1978: Ecological correlates of residence and non-residence in a Mediterranean passerine bird community. — J. Anim. Ecol. 47:871–890.

Hickey, J. J. 1952: Survival studies of banded birds. — USDI, Fish and Wildlife Serv. Spec. Sci. Rep., Wildlife No 15, Washington, D.C. 177 pp.

Holmes, R. T. & Sturges, F. W. 1975: Avian community dynamics and energetics in a northern hardwood ecosystem. — J. Anim. Ecol. 44:175–200.

Holyoak, D. 1971: Movements and mortality of Corvidae. — Bird Study 18:97–106.

Hutto, R. L. 1985: Habitat selection by nonbreeding, migratory land birds. — In: Cody, M. L. (ed.), Habitat selection in birds: 455–476. Academic Press Inc., Orlando, Florida.

Järvinen, O. & Väisänen, R. A. 1977a: Constants and formulae for analyzing line transect data. — Mimeogr., Helsinki, 10 pp.

— 1977b: Long-term changes of the North European land bird fauna. — Oikos 29:225–228.

Karr, J. R. 1976: On the relative abundances of north temperate migrants in tropical habitats. — Wilson Bull. 88:443–450.

Kipp, F. 1943: Beziehung zwischen dem Zug und der Brutbiologie der Vogel. — J. Ornithol. 91:144–153.

Klimkiewicz, M. K., Clapp, R. B. & Futcher, A. G. 1983: Longevity records of North American birds: Remizidae through Parulinae. — J. Field Ornithol. 54:287–294.

Klimkiewicz, M. K. & Futcher, A. G. 1987: Longevity records of North American birds: Coerebinae through Estrildidae. — J. Field Ornithol. 58:318–333.

Knapton, R. W. 1978: Breeding ecology of the Clay-colored Sparrow. — Living Bird 17:137–158.

Kulesza, G. 1990: An analysis of clutch-size in New World passerine birds. — Ibis 132:407–422.

Lack, D. 1950: Population ecology in birds: A review. — Proc. X Int. Orn. Congr. Uppsala, pp. 409–448.

Lanyon, S. M. & Thompson, C. F. 1986: Site fidelity and habitat quality as determinants of settlement pattern in male Painted Buntings. — Condor 88:206–210.

Leck, C. F., Murray, B. G. Jr. & Swinebroad, J. 1988: Long-term changes in the breeding bird populations of a New Jersey forest. — Biol. Conserv. 46:145–157.

Leisler, B. 1990: Selection and use of habitat of wintering migrants. — In: Gwinner, E. (ed.), Bird migration: 156–174. Springer-Verlag, Berlin Heidelberg.

Lindén, M. & Møller, A. P. 1989: Cost of reproduction and covariation of life history traits in birds. — Trends in Ecology and Evolution 4:367–371.

Linstedt, S. L. & Calder, W. A. 1976: Body size and longevity in birds. — Condor 78:91–94.

Mayfield, H. 1960: The Kirtland's Warbler. — Cranbrook Inst. Sci. Bull. 40. 242 pp.

Mönkkönen, M. & Helle, P. 1987: Avian reproductive output in European forest successions. — Oikos 50:239–246.

— 1989: Migratory habits of birds breeding in different stages of forest succession: a comparison between the Palaearctic and the Nearctic. — Ann. Zool. Fenn. 26:323–330.

Mönkkönen, M., Helle, P. & Welsh, D. 1992: Perspectives on Palaearctic and Nearctic bird migration: comparisons and overview of life-history and ecology of migrant passerines. — Ibis 134, Suppl. 1:7–13.

Morse, D. H. 1989: American warblers. An ecological and behavioural perspective. — Harvard University Press, Cambridge, Mass. 406 pp.

Murphy, M. T. 1989: Life history variability in North American breeding tyrant flycatchers: phylogeny, size or ecology. — Oikos 54:3–14.

Nilsson, S. G. 1982: Seasonal variation in the survival rate of adult nuthatches Sitta europea in Sweden. — Ibis 124:96–100.

Nolan, V. Jr. 1978: The ecology and behaviour of the Prairie Warbler Dendroica discolor. — Ecol. Monogr. 26:1–595.

O'Connor, R. J. 1981: Comparisons between migrant and non-migrant birds in Britain. — In: Aidley, D. J. (ed.), Animal migration: 167–195. Cambridge University Press, Cambridge.

Opdam, P., Rijsdijk, G. & Hustings, F. 1985: Bird communities in small woods in an agricultural landscape: Effects of area and isolation. — Biol. Conserv. 34:333–352.

Peters, R. H. 1983: The ecological implications of body size. — Cambridge University Press, Cambridge. 329 pp.

Rabøl, J. 1987: Coexistence and competition between overwintering Willow Warblers Phylloscopus trochilus and local warblers at Lake Naivasha, Kenya. — Ornis Scand. 18:101–121.

Rappole, J. H., Morton, E. S., Lovejoy, T. E. III & Ruos, J. L. 1983: Nearctic avian migrants in the Neotropics. — USDI, Fish and Wildlife Service, Washington, D. C. 384 pp.

Robbins, C. S. 1979: Effects of forest fragmentation on bird populations. — In: Management of north central and northeastern forests for nongame birds. USDA Forest Serv. Gen. Tech. Rep. NC-51:198–212.

Roberts, J. O. L. 1971: Survival among some North American wood warblers. — Bird-Banding 42:165–184.

Rosenberg, K. V. & Raphael, M. G. 1986: Effects of forest fragmentation on vertebrates in douglas-fir forests. — In: Verner, J., Morrison, M. & Ralph, C. J. (eds.), Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates: 263–272. Univ. of Wisconsin Press, Madison.

Rydzewski, W. 1978: The longevity of ringed birds. — Ring 96–97:218–262.

— 1979: The longevity of ringed birds. 2nd suppl. — Ring 100:70–72.

Sæther, B.-E. 1985: Variation in reproductive traits in European passerines in relation to nesting site: allometric scaling to body weight or adaptive variation? — Oecologia (Berl.) 68:7–9.

— 1987: The influence of body weight on the covariation between reproductive traits in European birds. — Oikos 48:79–88.

— 1988: Patterns of covariation between life-history traits of European birds. — Nature 331:616–617.

— 1989: Survival rates in relation to body weight in European birds. — Ornis Scand. 20:13–21.

SAS Institute Inc. 1988: SAS procedure guide, release 6.03 edition. — Gary, N. C. 441 pp.

Saurola, P. 1988: Bird ringing in Finland 1913–1987. (In Finnish with English summary.) — Lintumies 23:234–248.

Scott, S. L., Swinson, L. M., Dickinson, M. B. & Howell, C. H. (eds.) 1987: Field guide to the birds of North America. 2nd edition. — The National Geographic Society, Washington, D. C. 464 pp.

Searcy, W. A. & Yasukawa, K. 1981: Sexual size dimorphism and survival of male and female blackbirds (Icteridae). — Auk 98:457–465.

Sibley, C. G., Ahlquist, J. E. & Monroe, B. L. 1988: A classification of the living birds of the world based on DNA-DNA hybridization studies. — Auk 105:409–423.

Smith, S. 1975: Ecological aspects of dominance hierarchies in Black-capped Chickadees. — Auk 93:95–107.

Solonen, T. 1979: Population dynamics of the Garden Warbler Sylvia borin in southern Finland. — Ornis Fennica 56:3–12.

Southwood, T. R. E. 1976: Bionomic strategies and population parameters. — In: May, R. M. (ed.), Theoretical ecology: 30–52. Blackwell Scientific Publications, Oxford.

— 1977: Habitat, the templet for ecological strategies. — J. Anim. Ecol. 46:337–365.

— 1988: Tactics, strategies and templets. — Oikos 52:3–18.

Speirs, J. M. 1985: Birds of Ontario II. — Natural Heritage/Natural History Inc., Toronto.

Stewart, P. A. 1937: A preliminary list of bird weights. — Auk 54:324–332.

Terborgh, J. 1989: Where have all the birds gone? Essays on the biology and conservation of birds that migrate to the American tropics. — Princeton University Press, Princeton.

Virkkala, R. 1990: Effects of forestry on birds in a changing north-boreal coniferous landscape. — Ph. D. Thesis, Univ. of Helsinki, Helsinki. 13+78 pp.

Western, D. & Ssemakula, J. 1982: Life history patterns in birds and mammals and their evolutionary interpretation. — Oecologia (Berl.) 54:281–290.

Westneat, D. F. 1986: The effects of muscle biopsy on survival and condition in White-throated Sparrows. — Wilson Bull. 98:280–285.

Westneat, D. F., Payne, R. B. & Doehlert, S. M. 1986: Effects of muscle biopsy on survival and breeding success in Indigo Buntings. — Condor 88:220–227.

Whitcomb, R. F., Robbins, C. S., Lynch, J. F., Whitcomb, B. L., Klimkiewicz, M. K. & Bystrak, D. 1981: Effects of forest fragmentation on avifauna of the eastern deciduous forest. — In: Burgess, R. L. & Sharpe, D. M. (eds.), Forest island dynamics in man-dominated landscapes: 125–205. Springer-Verlag, New York.

Wilkinshaw, L. H. 1966a: Studies of the Acadian Flycatcher in Michigan. — Bird-Banding 37:227–257.

— 1966b: Summer biology of the Traill's Flycatcher. — Wilson Bull. 78:31–46.

Zammuto, R. M. 1986: Life histories of birds: clutch size, longevity, and body mass among North American game birds. — Can. J. Zool. 64:2739–2749.

Appendix. Survival rate estimates (S) for North American and European passerine bird genera, with average body weights (W) and sources of survivorship information. Migratory habit (M): T = tropical migrant, O = other.

Genus	M	S	W	Source
North America:				
Tyrannus	T	0.48	44	Blancher & Robertson 1985
Empidonax	T	0.52	12	Wilkinshaw 1966a, b, Greenberg 1980
Lanius	O	0.52	60	Haas & Sloane 1989
Vireo	T	0.39	13	Leck et al. 1988
Cyanocitta	O	0.55	87	Hickey 1952
Hylocichla	T	0.38	52	Leck et al. 1988
Turdus	O	0.58	80	Farner 1955
Dumetella	O	0.52	39	Darley et al. 1977
Toxostoma	O	0.35	83	Haas & Sloane 1989
Troglodytes	O	0.42	10	Drilling & Thompson 1988
Parus	O	0.26	14	Elder 1985, Smith 1975
Carpodacus	O	0.52	22	Farner 1955
Melospiza	O	0.55	18	Farner 1955
Passerculus	O	0.38	17	Bedard & LaPointe 1984
Passerina	T	0.67	16	Lanyon & Thompson 1986, Westneat et al. 1986
Pipilo	O	0.22	42	Leck et al. 1988
Pooecetes	O	0.56	24	Best & Rodenhouse 1984
Spizella	T	0.72	12	Knapton 1978
Zonotrichia	O	0.49	33	Baker et al. 1981, Westneat 1986
Dendroica	T	0.56	11	Mayfield 1960, Roberts 1971, Eliason 1986
Dendroica	O	0.64	10	Nolan 1978
Geothlypis	O	0.54	11	Roberts 1971
Mniotilta	O	0.71	11	Roberts 1971
Seiurus	T	0.79	20	Roberts 1971
Setophaga	T	0.71	9	Roberts 1971
Vermivora	O	0.50	9	Greenberg 1980
Wilsonia	T	0.71	11	Roberts 1971
Cardinalis	O	0.32	42	Leck et al. 1988
Dolichonyx	T	0.49	36	Gavin & Bollinger 1988
Agelaius	O	0.52	65	Searcy & Yasukawa 1981
Euphagus	O	0.54	60	Searcy & Yasukawa 1981
Icterus	T	0.55	32	Searcy & Yasukawa 1981

Appendix cont.

Genus	M	S	W	Source
Molothrus	O	0.42	42	Searcy & Yasukawa 1981
Quiscalus	O	0.66	115	Searcy & Yasukawa 1981
Xanthocephalus	O	0.58	49	Searcy & Yasukawa 1981
Europe:				
Corvus	O	0.64	604	Holyoak 1971, Dobson 1990
Garrulus	O	0.74	161	Dobson 1990
Pica	O	0.71	235	Dobson 1990
Turdus	O	0.54	91	Haukioja 1969, Sæther 1989, Dobson 1990
Ficedula	T	0.42	12	Gustafsson 1985, Dobson 1990
Erithacus	O	0.46	17	Dobson 1990
Luscinia	O	0.46	22	Czarnecki 1975
Phoenicurus	T	0.49	15	Haukioja 1969
Phoenicurus	O	0.29	15	Czarnecki 1975
Saxicola	T	0.46	16	Sæther 1989
Sturnus	O	0.48	77	Coulson 1960
Sitta	O	0.50	23	Nilsson 1982
Troglodytes	O	0.32	9	Dobson 1990
Parus	O	0.55	12	Ekman 1984, Dobson 1990
Aegithalos	O	0.47	8	Dobson 1990
Delichon	T	0.34	17	Dobson 1990
Hirundo	T	0.36	19	Dobson 1990
Riparia	T	0.35	14	Dobson 1990
Regulus	O	0.14	6	Dobson 1990
Phylloscopus	T	0.40	9	Dobson 1990
Phylloscopus	O	0.50	8	Dobson 1990
Acrocephalus	T	0.45	12	Dobson 1990
Sylvia	T	0.32	19	Solonen 1979, Dobson 1990
Sylvia	O	0.42	15	Dobson 1990
Alauda	O	0.65	37	Sæther 1989
Passer	O	0.50	28	Dobson 1990
Anthus	T	0.41	23	Sæther 1989
Anthus	O	0.60	22	Dobson 1990
Motacilla	T	0.48	18	Dobson 1990
Motacilla	O	0.47	20	Dobson 1990
Prunella	O	0.46	19	Dobson 1990
Fringilla	O	0.61	22	Dobson 1990
Carpodacus	T	0.44	23	Czarnecki 1975
Carduelis	O	0.47	15	Dobson 1990
Chloris	O	0.57	29	Haukioja 1969
Coccothraustes	O	0.40	53	Czarnecki 1975
Pyrrhula	O	0.51	31	Dobson 1990
Emberiza	O	0.53	25	Dobson 1990