Parasitism as a migration cost

ORIOL CLARABUCH, JACOB GONZÁLEZ-SOLÍS

SUMMARY - Migration costs are usually evaluated in terms of energy expenditure or risk of predation. Although parasitism has been widely recognized as an important potential factor for fitness, only a few studies have dealt with the relationships between migration and parasitism. From 1991 to 1997 birds in the surroundings of Santa Susanna village (Catalan Mediterranean coast) were regularly mist-netted and ringed. Blood smears from 13 common passerine species were collected during the reproductive period and examined to detect the presence of blood parasites. Migratory status of these species was assigned according to the analysis of captures and recaptures over the year. Some samples of diptera were also collected with a Malaise trap installed near the ringing station and determined to species level. Five bird species were classified as migrants and 8 species were classified as resident. In four of the five migrant species, at least one individual infected by haematozoan parasites was found. Among the eight resident species, only one species showed infected individuals. At least three species of dipteran were identified in the study area as a potential vector for haematozoan haemoproteids. We suggest two ways to explain these results. 1.- *The habitat-heterogeneity hypothesis*: the degree of exposure of host species to parasite vectors has been reported as one of the main factors to explain parasite prevalences. In spite of the presence of potential vectors in the study area, haematozoan parasites seem to be absent from the area. Migratory species were parasitized outside the study area in the winter quarters or at the stop-over sites during migration. 2.- *The immunosuppressive hypothesis*: immunosupressive effects of large energy investment of host species can increase the level of infection. Resident species are not so stressed as migratory species. Resident species, although infected, can maintain parasite infection below the detectability level or they can recover from infections. Migratory species are more likely to develop acute infections as a consequence of the migratory effort.

RIASSUNTO - **Il parassitismo come costo legato alla migrazione.** I costi legati alla migrazione vengono generalmente valutati in termini di dispendio energetico o rischio di predazione. Sebbene il parassitismo sia stato ampiamente riconosciuto quale un importante fattore per la fitness, solo pochi studi hanno finora trattato le correlazioni tra migrazione e parassitismo. Dal 1991 ed il 1997 sono state condotte regolari attività di inanellamento nei dintorni del villaggio di Santa Susanna (costa mediterranea catalana). Strisci di sangue raccolti da 13 specie comuni di Passeriformi nel corso del periodo riproduttivo sono stati esaminati per verificare l'eventuale presenza di parassiti ematici. Il comportamento migratorio delle singole specie è stato determinato in base all'analisi dei dati di cattura/ricattura nel corso dell'anno. Per mezzo di trappole Malaise installate nei pressi della stazione di inanellamento sono anche stati raccolti campioni di Ditteri, determinati a livello specifico. Cinque specie di uccelli sono state classificate migratrici ed 8 residenti. In quattro delle cinque specie migratrici è stato osservato almeno un individuo infestato da ematozoi; tra le otto specie residenti, solo una specie ha mostrato individui infetti. Nell'area di studio sono state identificate almeno tre specie di ditteri quali potenziali vettori di protozoi appartenenti al gruppo *Haemoproteus*; vengono suggerite due teorie per interpretare questi risultati. 1.- L'ipotesi di eterogeneità ambientale: il grado di esposizione della specie ospite ai vettori di parassiti è stato citato quale uno dei principali fattori che spiegano la prevalenza parassitaria. Nonostante la presenza di potenziali vettori nell'area di studio, ematozoi parassiti sembrano essere assenti dall'area di studio. Le specie migratrici sono quindi state parassitate al di fuori dell'area di studio, nei quartieri di svernamento o nelle aree di sosta nel corso della migrazione. 2.- L'ipotesi immunosoppressiva: effetti immunosoppressivi legati ad importanti investimenti energetici della specie ospite possono aumentare il livello di infezione. Le specie residenti non sono stressate quanto quelle migratrici; esse, sebbene infette, sono in grado di mantenere la carica parassitaria al di sotto della soglia di deteminabilità o possono guarire dalle infezioni. Le specie migratrici sono più soggette a sviluppare infezioni acute come conseguenza dello sforzo legato alla migrazione.

INTRODUCTION

Costs of migration are usually evaluated in terms of energy expenditure or risk of predation (e.g. Lindström 1989, Alerstam & Lindström 1990, Videler 1995). Although parasitism has been widely recognized as an important potential factor for fitness (see review in Møller 1997), only a few studies have dealt on the relationship between migration and parasitism (Ashford 1971, Peirce & Mead 1978, Valkiunas 1993, McNeil *et al.* 1995, Garvin & Remsen 1997, Møller & Erritzøe, *in press*). The transmission of parasites depends greatly on the host isolation. It is believed that a greater geographic range of the host increases the likelihood of hosts to be in contact with more potential intermediate hosts (e.g. Bell & Burt 1991). Therefore, noticeable interactions between parasites and migration could be expected. Nevertheless it is surprising that the parasite ecology literature has given scant attention to this subject. A reason for this gap is that the degree of isolation of host is usually difficult to measure, both at intra and inter-specific level (Simberloff & Moore 1997). Host isolation is not only dependent on the geographic range of the host but also on the geographic range of the vectors. However, bird migration provides a singular opportunity to compare different host geographic ranges, since resident and migratory species show clearly different geographic ranges. Moreover, the geographic range of migrant birds is large enough to minimize the potential influence of vector movement on host isolation.

In this study, we examine the relationship between blood parasite prevalences and the migratory status of 13 common passerine species on the Catalan Mediterranean coast.

MATERIAL AND METHODS

From 1991 to 1997 birds in the surroundings of Santa Susanna village (Catalan Mediterranean coast) were regularly mist-netted and ringed. Additionally, in 1996 and 1997 blood smears from 13 passerine species (Table 1) were collected between April and July by venipuncture of the radial vein. Smears were air-dried and fixed for 10 minutes in methanol on the day of sampling. In the laboratory the slides were stained with GIEMSA and examined to detect the presence of blood parasites under a microscope with oil at 1,000x. Smears were scored by one observer. Prevalence was established through the inspection of 100 fields containing about 100 erythrocytes per sample. *Haemoproteus* genus was identified following Bennett *et al.* (1992a). No other genus of blood parasites were found, although the possibility that some *Plasmodium* were misidentified as *Haemoproteus* cannot be discarded due to the weak stain of some of the smears (personal communication from Reija Dufva after checking some of the smears).

All birds were older than 1 year and the species analyzed are short-lived, therefore, potential biases coming from different exposure depending on the age (Weatherhead & Bennett 1991, Allander & Bennett 1994) were minimized.

Among the 13 species (Table 1), three were trans-Saharan migrants (Willow Warbler *Phylloscopus trochilus*, Melodious Warbler *Hippolais polyglotta* and the Swallow *Hirundo rustica* (Curry-Lindahl 1981) and three largely resident (Crested Tit *Parus cristatus*, Short-toed Treecreeper *Certhia brachydactyla* and House Sparrow *Passer domesticus*). The rest are usually considered as partial migrants (Berthold 1993), so we used the retrap data in order to clarify their migratory status in our study area. Those having some retraps between the summer (April to July) and wintering periods (November to February) were considered residents, meanwhile those without interperiod retraps were considered migrants (Table 1). The Blackcap *Sylvia atricapilla* was considered a non-trans-Saharan migrant since the western populations are mainly wintering in the Iberian peninsula and Maghreb, although the trans-Saharan route can be considered as a subsidiary one (Berthold 1993).

During April 1996 a Malaise trap was installed to capture the most common species of diptera in the study area for a qualitative analysis. This trap does not have any attracting agent, but intercepts flying insects which are passively led into a container of killing and preservative agent. Thus, this method ensures that the captured diptera come from the study area. The collected insects were analyzed and the species of diptera belonging to the genus *Culicoides* were identified.

Independence among migratory status and prevalence was tested by a contingency table. As minimum expected frequencies were lower than 5, a Fisher's exact test was used. All tests were two-tailed. As host species from the same lineage are not truly independent, the phylogenetic relationships of host species should be controlled (Poulin 1995). However, the small number of bird species examined was not enough to control for phylogeny.

RESULTS

The migratory status of the 13 species examined is shown in table 1. A total of 188 smears from the 13 bird species were examined. Five species were infected by haematozoan parasites from the genus *Haemoproteus*. No other blood parasites were found. Sample size for each bird species and parasite prevalences are shown in table 1. Among the five species classified as migrants, the three trans-Saharan ones showed at least one individual infected. Among the eight species classified as residents only the

Species	N captured	% recaptured	Migratory status	N smears	N infected	% infected
Turdus merula	41	22.0	R	20	3	15
Sylvia melanocephala	14	64.3	R	6	0	0
Aegithalos caudatus	17	52.9	R	10	0	0
Parus cristatus	9	22.2	R	7	0	0
Parus caeruleus	30	26.7	R	20	0	0
Parus major	34	23.5	R	20	0	0
Certhia brachydactyla	21	38.1	R	15	0	0
Passer domesticus	17	11.8	R	9	0	0
Erithacus rubecula	21	0	M	20	0	0
Sylvia atricapilla	28	0	M	19	3	15.8
Phylloscopus trochilus	15	0	TM	4	1	25
Hippolais polyglotta	36	0	TM	20	14	70
Hirundo rustica	22	0	TM	18	2	11.1

Table 1 - Migratory status and prevalences of *Haemoproteus sp.* in 13 passerine species from Santa Susanna (Catalan Mediterranean coast, Spain). Migratory status: R= resident, M= migrant, TM= trans-Saharan migrant.

Blackbird *Turdus merula* showed infected individuals. The number of bird species with at least one infected individual was not independent from the migratory status (Fisher's Exact test $P<0.05$). Results show that migratory species were significantly more infected than resident ones (Table 1). Similarly, the number of trans-Saharan migrants with at least one infected individual was significantly higher than the rest of the species (Fisher's Exact test $P<0.05$). If Blackcap *S. atricapilla* was considered a trans-Saharan migrant differences would be even more significant (Fisher's Exact test $P<0.01$).

From the sample of diptera analyzed three different ornithophilic biting midges of the genus *Culicoides* were found: *C. pictipennis*, *C. sylvarum* and *C. obsoletus*.

DISCUSSION

In spite of the small number of bird species examined in our study there were significantly more migratory species infected by *Haemoproteus sp.* than resident ones. A low incidence of parasites of the genus *Haemoproteus* in non-migratory passerines has been reported (Peirce & Mead 1978, Valkiunas 1993 and references thererin). We suggest two ways to explain these differences already pointed out by Peirce and Mead (1978): the habitat-heterogeneity hypothesis and the immunosuppressive hypothesis.

The habitat-heterogeneity hypothesis

Although vector abundance is seldom measured, the degree of exposure of host species to parasite vectors has been reported as one of the main factors to explain parasite prevalences, both within and among species. Haematozoan parasites are transmitted by blood-feeding diptera (e.g. Janovy 1997) which differ in abundance depending on the habitat or microhabitat. Typically, bird prevalences are low in unsuitable environments for vectors, like islands far away from the mainland and hence, difficult to reach by parasite vectors (Little & Earlé 1994, González-Solís & Abella 1997). Likewise, interspecific differences in bird prevalences according to vertical stratification of nesting or foraging sites (Bennett & Fallis 1960, Greiner *et al.* 1975, Pruett-Jones *et al.* 1991, Garvin & Remsen 1997) or nesting habitats (Bennett *et al.* 1992b) seem to be related to the abundance and activity of vectors. Within species, inter-annual and inter-population variability in prevalence values seems to be a consequence of differences in vector densities among years and geographic areas (van Riper 1991, Allander & Bennet 1994, Bennett *et al.* 1995, Ruiz *et al.* 1995). Similarly, older birds are usually more often infected, presumably as a result of both a longer time exposure to vectors and to different habitat types (Weatherhead & Bennett 1991, Allander & Bennett 1994). Another source of variability in exposure to vectors is the host's geographic range. Increased range of hosts leads to visit greater heterogeneity of habitats and therefore, hosts comes into contact with more potential vectors or with other birds from whom they can be infected through host transfer (Bartoli 1989, Jones 1991, Simberloff & Moore 1997 and references therein). Thus, it could be expected that migratory species will show larger prevalences than non-migratory ones.

It is believed that haematozoan infections are acquired primarily on the breeding grounds (Beaudoin *et al.* 1971). If this is true, no difference in prevalences would be expected between migrant and non-migrant species with similar summer habitats. This seems to be the case with Garvin & Remsen (1997) who did not find any relationship between the prevalence levels and the migratory status of 19 bird species from Louisiana (USA). However, it has been shown that wintering areas can also be suitable places for local transmission of parasites: birds migrating from the White Sea were infected in the wintering Baltic Sea area, where the relatively warm winter would favour the vectors and therefore the local transmission of haematozoan parasites between birds (cited in Crompton 1997). According to our data, migrant species showed higher prevalences than resident ones, suggesting that differences may emerge from the exposure in wintering grounds of the migratory species. However, differences in exposure between resident and migrant species might also arise from different breeding habitats, since the patterns of breeding habitat are different (Fuller & Crick 1992).

Stop-overs during migration could also increase the probability of birds to be infected. Few bird species cover the whole migratory distance in one stage, especially long-distance migrants whose travels in autumn may last for months (e.g. Pearson & Lack 1992, Berthold 1996). In fact, migration stop-overs fit as another example of the habitat-heterogeneity argument (Simberloff & Moore 1997). Long-distance migrants should present higher prevalences since they visit more varied habitats. Moreover, we believe that high prevalences of parasites in the intermediate host could be expected at the stop-over sites, since many bird species use quite narrow corridors and geographical bottlenecks during migration year after year (Biebach 1990, Pearson & Lack 1992), probably favouring local transmission of parasites. Trans-Saharan migrants show higher prevalences in Great Britain (Bennett *et al.* 1974, Peirce & Mead 1978). In our study, all three trans-Saharan species examined showed at least one individual infected whilst among the 10 remaining species only three species showed infected birds.

Parasites from the genus *Haemoproteus* have been defined elsewhere for all bird species analyzed here. Hence, any population of these species could be infected by haemoproteids. Nevertheless, incidence of blood parasites between populations are highly variable ranging from populations virtually free from haematozoa to populations where nearly all birds are infected (e.g. Korpimäki *et al.* 1993, Bennett *et al.* 1995, Ruiz *et al.* 1995). Supporting Bennett *et al.* (1974), Peirce & Mead (1978) suggested that low incidence of haemoproteids in non-migrant passerines was due to the absence of suitable vectors in their study area. However, in our study area we identified three different species of *Culicoides* that are presumably capable of local transmission of haemoproteids (Bennett *et al.* 1992a). This suggest that Haematozoan parasites and not the vectors are lacking in the study area. As the dispersion of the vectors is certainly limited to local movements, the dispersion of the haematozoan parasites rely on the geographic range of the bird species. Actually, little is known about the impact of migration as a dispersal agent of bird parasites (Crompton 1997). The scarcity of parasites in the study area, in spite of the presence of the vectors, supports the idea that the lower infection levels for resident bird species are a consequence of their restricted geographic range, avoiding to come into contact with other infected populations.

The immunosuppressive hypothesis

Immunosuppressive effects of large energy investments in host species, for instance high reproductive effort, may directly decrease immune responsiveness to parasites. Several experiments have shown that an artificial increase in parental investment by the manipulation of brood size can influence the susceptibility to haematozoan parasitemias (Norris *et al.* 1994, Richner *et al.* 1995, Allander 1997). However, it is surprising that effects of migration effort on parasitism have not been scrutinized. Flight is an expensive method of locomotion (Alerstam 1991) and energy cost of migration can exceed the cost of reproduction (Drent & Piersma 1990). Migration appears to be physically exhausting especially when birds cross ecological barriers such as seas or deserts, leading to lipid depletion (e.g. Bairlein 1991, Bairlen & Simons 1995). Although we can only speculate in which way migration affects the immunocompetence, it is evident that such an energy-demanding activity may produce a recrudescence of latent infections acquired in the past years.

If this hypothesis is true, the scarcity of parasite infections in resident species compared to migrant species would reflect resistance, capacity to recover from the infections or capacity to maintain the chronic infections below the detectability levels rather than lack of parasites or exposure to vectors. Usually, birds tend to retain their parasite infections over years (Weatherhead & Bennett 1991) and it is quite likely that latent infections can be maintained on a low-grade nonpathogenic level below the detectability for long periods. Then, we could assume relatively similar prevalence values for all bird species investigated and the same initial capacity to maintain the infection below the detectability level. Thus, if migration effort increase susceptibility to parasitism, then the prevalence of parasites should be higher in migrant species and especially in trans-Saharan birds, as certainly shown by the data. The fact that resident species were so poorly infected in spite of the presence of potential vectors could also support this hypothesis.

However, if resident species are also infected, parasites should be apparent during the breeding season, i.e. when chronic infections usually relapse (Weatherhead & Bennet 1991). However, among the eight resident species analyzed, only one showed infected individuals. Although lower levels of prevalences and intensities in resident species could be expected, the scarcity of parasitemias in resident species even during the breeding period seems to support the habitat-heterogeneity hypothesis.

Our data neither strongly supports nor refute any of the two hypotheses. In fact, the two hypotheses are not mutually exclusive and separating them can be difficult because it seems to require the separation between the migration effort and exposure during migration. Clearly, more studies are needed to reveal the relationships between migration and parasitism, both between and within species.

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Oriol Clarabuch[1], Jacob González-Solís[1, 2]

[1] *Departament de Biologia Animal (Vertebrats). Universitat de Barcelona. Diagonal 645. Barcelona 08028, Spain.*

[2] *Present address: Institut für Vogelforschung "Vogelwarte Helgoland", An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany.*