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LEAPFROG MIGRATION IN NORTH AMERICAN SHOREBIRDS: INTRA- AND INTERSPECIFIC EXAMPLES[1]

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Abstract. A method that detects leapfrog migration is described. It emphasizes the two-step process of leapfrog migration: the seasonal switching of latitudinal ranges and the latitudinal segregation of taxa. The method was used to make a systematic search for leapfrog migration patterns among the North American shorebirds (suborder: Charadrii). One case of intraspecific leapfrog migration, within the Rock Sandpiper *Calidris ptilocnemis,* and several cases of interspecific leapfrog migration, within *Numenius, Limosa, Arenaria, Calidris,* Charadriini, Numeniini, Calidridini, Scolopacidae, and Charadrii, were revealed. In most cases, smaller species leapfrog larger species.

Key words: Leapfrog migration; migration; New World; North American migrants; shorebirds.

INTRODUCTION

Leapfrog migration is an unusual migration pattern in which a more northerly group during summer, migrates beyond another group, to become the more southerly group during winter (Welty 1982). Swarth (1920) was the first to describe a leapfrog migration pattern. In what has become the classic example of leapfrog migration, he showed that it occurs among the six subspecies of the Fox Sparrow, *Passerella iliaca,* in North America. Since then only a few other leapfrog migration patterns have been described. These have included both intraspecific patterns (i.e., between or among subspecies; Swarth 1920, Stresemann 1934, Salomonsen 1955, Pienkowski et al. 1985) and interspecific patterns (i.e., between or among species; Lack 1944, Cody and Walter 1976, Alerstam and Hogstedt 1980).

Mayr and Meise (1930) were the first to consider the reasons for leapfrog patterns and decided that there was "no clear reason why northern populations should not stop in the northern part of the winter range." Since then three basic hypotheses have been put forward: the Competition Hypothesis (Salomonsen 1955, Pienkowski et al. 1985), the Spring Predictability Hypothesis (Alerstam and Hogstedt 1980, 1985), and the Time Allocation Hypothesis (Greenberg 1980). Each of these hypotheses has been criticized (Slagsvold 1982, Pienkowski et al. 1985, Myers et al. 1985) and, at present, there is no consensus as to why leapfrog migration occurs.

I contend that even before we test these hypotheses, we need to solve two problems relating to the investigation of leapfrog migration. First, there is no established method for determining leapfrog migration; many interspecific leapfrog migration patterns have been determined by inspection and most are for two species chosen haphazardly from many co-occurring congeners (Lack 1944, Alerstam and Hogstedt 1980). Second, so few examples of leapfrog migration have been documented that it is difficult to know how widespread the phenomenon is.

In an attempt to resolve these problems I devised a method for determining leapfrog migration and searched for examples of leapfrog migration within a large group of co-occurring birds, the North American shorebirds (suborder: Charadrii). It is a promising group within which to search because there are many species, most of which are migrants (Johnsgard 1981), and leapfrog migration has been observed within and between a few shorebird species in other parts of the world (Lack 1944, Salomonsen 1955, Alerstam and Hogstedt 1980, Pienkowski et al. 1985).

I have looked for both intra- and interspecific leapfrog migration patterns. Interspecific leapfrog migration occurs between (or among) similar species, but the question of how taxonomically similar these species need to be has not been addressed. Therefore I have looked for interspecific leapfrog patterns among (or between) species within the genus, the tribe, the family, and the

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suborder. In addition, I determine whether there are any patterns in the latitudinal distribution of species of different sizes in the examples of interspecific leapfrog migration that this study reveals. Whether or not a size distribution occurs in all cases of leapfrog migration is important, because the Competition Hypothesis as amended by Pienkowski et al. (1985) is based on the observation that in some cases of leapfrog migration, the winter distribution of the taxa is such that the smaller taxon winters farther south (e.g., Pienkowski et al. 1985).

METHODS

The major features of leapfrog migration are the seasonal switching of latitudinal ranges and the low overlap of these ranges (Swarth 1920). The method that I have used to detect leapfrog migration calculates the extent of seasonal switching and the extent of latitudinal overlap, and defines leapfrog migration as occurring when both of these values are beyond a certain cutoff point.

The degree to which seasonal switching of the latitudinal ranges occurs within a group of species (or subspecies) was determined by comparing, using Spearman's rank correlation analysis (Sokal and Rohlf 1981), the species' breeding and wintering mid-latitudes. Correlation is expressed by a coefficient (r) that ranges from -1 to $+1$. I have called r values of -0.8 to -1.0 "good switching"; -0.35 to -0.79 "partial switching"; and >-0.34 "nonswitching." In the classic example of leapfrog migration in North American Fox Sparrows (Swarth 1920) the r value is -0.70, i.e., partial switching (calculated from the original data by Boland).

The degree to which the species (or subspecies) within a group overlap latitudinally was estimated by calculating the overlap between species' winter ranges. I divided each species' winter range into 5° latitude segments and assumed equal occupation of all segments. I calculated the degree of overlap for all pairs of species within the group, using the Percent Similarity Index (Schoener 1970) and then averaged these values for the group. Species within a group were considered latitudinally segregated if their mean overlap was less than 0.40. For the group of North American Fox Sparrow subspecies the mean overlap is 0.27 (calculated from Swarth 1920, by Boland).

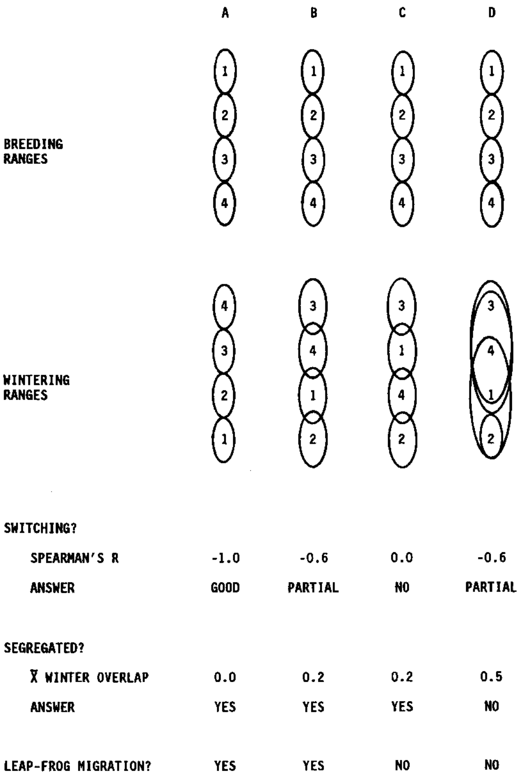

FIGURE 1. Illustration of method used for determining leapfrog migration. The breeding and wintering ranges are given for 16 hypothetical species. Leapfrog migration occurs in situations A and B, but not in C and D.

Figure 1 illustrates these methods using the distributions of 16 hypothetical species. Leapfrog migration occurs in A and B because switching is good or partial, and the species are well segregated in winter. Leapfrog migration does not occur in C and D because switching does not occur in C, and the species winter overlaps are high in D.

Forty-seven species of shorebirds breed in North America and winter in the New World (Johnsgard 1981, AOU 1983, see Boland 1988 for list of species). Twelve of these species have two or more subspecies that breed and winter in the New World (Johnsgard 1981, AOU 1983). The species' and subspecies' breeding ranges were taken from Johnsgard (1981) and winter ranges were estimated primarily from AOU (1983) with additional information from Blake (1977) and Johnsgard (1981). Breeding and wintering mid-latitudes were calculated for each subspecies and species as the latitudes midway between the northern and southern limits of their breeding and wintering ranges, respectively. (Breeding and

TABLE 1. Intraspecific leapfrog migration. The extent to which switching of latitudinal ranges and segregation of winter ranges occur within the North American shorebird species. n = number of subspecies, r = Spearman's rank correlation coefficient, and $\bar{x}$ = mean overlap in winter ranges.

		Switching?		Segregated?	Leapfrog
Species	n	r		$\bar{x}$	migration?
1 Wilson's Plover (*Charadrius wilsonia*)	4	0.40	no	0.44	no
2 Killdeer (*C. vociferus*)	3	1.00	no	0.27	no
3 Piping Plover (*C. melodus*)	2	−1.00	good	0.66	no
4 Snowy Plover (*C. alexandrinus*)	2	−1.00	good	0.51	no
5 Solitary Sandpiper (*Tringa solitaria*)	2	−1.00	good	0.63	no
6 Willet (*Catoptrophorus semipalmatus*)	2	−1.00	good	0.72	no
7 Long-billed Curlew (*Numenius americanus*)	2	1.00	no	0.85	no
8 Ruddy Turnstone (*Arenaria interpres*)	2	1.00	no	1.00	no
9 Rock Sandpiper (*Calidris ptilocnemis*)	3	−0.50	partial	0.37	yes
10 Dunlin (*C. alpina*)	2	1.00	no	0.70	no
11 Short-billed Dowitcher (*Limnodromus griseus*)	3	0.87	no	0.73	no
12 Common Snipe (*Gallinago gallinago*)	3	1.00	no	0.16	no

wintering ranges and mid-latitudes are given in Boland 1988.)

Patterns in the latitudinal distribution of body sizes within a group were determined by comparing, using Spearman's rank correlation analysis (Sokal and Rohlf 1981), the species' mean body size with both their breeding and their wintering mid-latitudes. A pattern was considered valid if the coefficient, r, was less than −0.35 or more than 0.35. Mean body weight for each species was calculated from data in Johnsgard (1981), Page et al. (1979), Johnson (1979), and Cramp and Simmons (1983).

RESULTS

INTRASPECIFIC LEAPFROG MIGRATION PATTERNS

Twelve North American species have two or more subspecies that breed and winter in the New World. Seasonal switching of latitudinal ranges occurs within five of these species (Table 1) but overlap of the subspecies' winter ranges is low in only one of these, the Rock Sandpiper (*Calidris ptilocnemis*; Table 1). Thus intraspecific leapfrog migration occurs within only the Rock Sandpiper.

INTERSPECIFIC LEAPFROG MIGRATION PATTERNS

I have considered the species within different taxonomic groups. The species within four of the 10 genera show leapfrog migration patterns: namely the genera *Numenius, Limosa, Arenaria,* and *Calidris* (Table 2A).

The species within five of the nine tribes show leapfrog migration patterns (Table 2B). Some of these groups are identical to the genus groups and are marked with an asterisk in Table 2. Thus, leapfrog migration occurs within three of the four new groups at this level (Charadriini, Numeniini, and Calidridini; Table 2B).

At the level of the family, the species within two of the four families show leapfrog migration patterns (Charadriidae and Scolopacidae; Table 2C). Finally at the level of the suborder, leapfrog migration occurs among all 47 North American shorebird species (Table 2D).

It is possible that the strong switching pattern within the Calidridini (Table 2B), the tribe con-

TABLE 2. Interspecific leapfrog migration. The extent to which switching of latitudinal ranges and segregation of winter ranges occur within the North American shorebird groups. n = number of species in group, r = Spearman's rank correlation coefficient, $\bar{x}$ = mean overlap in species' winter ranges, and * = groups in which the component species are not different from a lower taxonomic level.

Group	n	Switching?		Segregated?	Leapfrog migration?
		r		$\bar{x}$	
A. Within genera					
1 *Haematopus*	2	1.00	no	0.24	no
2 *Pluvialis*	2	1.00	no	0.30	no
3 *Charadrius*	6	0.03	no	0.42	no
4 *Tringa*	3	0.50	no	0.82	no
5 *Phalaropus*	3	−0.50	partial	0.74	no
6 *Numenius*	3	−1.00	good	0.18	yes
7 *Limosa*	2	−1.00	good	0	yes
8 *Arenaria*	2	−1.00	good	0.18	yes
9 *Calidris*	12	−0.45	partial	0.30	yes
10 *Limnodromus*	2	1.00	no	0.48	no
B. Within tribes					
* Haematopodini	2	1.00	no	0.24	*
11 Charadriini	8	−0.50	partial	0.35	yes
12 Tringini	6	0.01	no	0.70	no
* Phalaropini	3	−0.50	partial	0.74	*
13 Numeniini	4	−0.80	good	0.30	yes
* Limosini	2	−1.00	good	0	*
* Arenariini	2	−1.00	good	0.18	*
14 Calidridini	14	−0.52	partial	0.30	yes
* Limnodromini	2	1.00	no	0.48	*
C. Within families					
* Haematopodidae	2	1.00	no	0.24	*
15 Recurvirostridae	2	1.00	no	0.48	no
* Charadriidae	8	−0.50	partial	0.35	*
16 Scolopacidae	35	−0.36	partial	0.35	yes
D. Within the suborder					
17 All North American species	47	−0.42	partial	0.36	yes

taining the most species, biases the Spearman's ranking towards switching in the family Scolopacidae and the suborder. However, even without the Calidridini, both the Scolopacidae and the suborder show partial switching patterns (−0.39 and −0.45, respectively).

This analysis has revealed several cases of interspecific leapfrog migration within the North American shorebirds at taxonomic levels from genus to suborder. The patterns are strongest in the taxa with few species; i.e., the genera *Numenius* (three species), *Arenaria* (two species), and particularly *Limosa* (two species). Nevertheless, leapfrog migration also occurs within several multispecies taxa (e.g., *Calidris*; 12 species) and the suborder as a whole (47 species).

Next I looked for trends in the latitudinal distribution of body sizes within the leapfrog taxa. In general, smaller species breed farther north, and winter farther south than larger species. Within six of the nine leapfrog taxa there is a strong trend for the smaller species to breed farther north, and within four of these taxa the smaller species also winter farther south (Table 3). These trends are particularly strong within the genera *Numenius, Arenaria,* and *Limosa.* Within these genera in particular and the leapfrog taxa in general, the smaller species leapfrog the larger species. In the nonleapfrog taxa the results are less clear, but, in general, the smaller species are distributed farther south than the larger species during both seasons.

DISCUSSION

The method I have devised to detect leapfrog migration patterns is useful because it empha-

TABLE 3. Relationships between latitude and shorebird body weight using Spearman's rank correlation (r) analysis. When $r > 0.35$ smaller species are distributed farther south than larger species; when $r < -0.35$ smaller species are distributed farther north than larger species; and when an r value is between 0.35 and −0.35 there is no pattern in the distribution of small and large species (—).

		Summer distribution		Winter distribution	
Taxon	n	r	Smaller species farther	r	Smaller species farther
A. Leapfrog taxa[1]					
6 *Numenius* (g)	3	−1.00	north	1.00	south
7 *Limosa* (g)	2	−1.00	north	1.00	south
8 *Arenaria* (g)	2	−1.00	north	1.00	south
9 *Calidris* (g)	12	0.17	—	0.10	—
11 Charadriini (t)	8	0.54	south	−0.26	—
13 Numeniini (t)	4	−0.40	north	0.80	south
14 Calidridini (t)	14	0.01	—	0.10	—
16 Scolopacidae (f)	35	−0.33	north	0.12	—
17 Charadrii (so)	47	−0.25	north	0.10	—
$\bar{x}$		−0.36	north	0.44	south
B. Nonleapfrog taxa					
1 *Haematopus* (g)	2	1.00	south	1.00	south
2 *Pluvialis* (g)	2	1.00	south	1.00	south
3 *Charadrius* (g)	6	−0.09	—	0.37	south
4 *Tringa* (g)	3	0.00	—	0.87	south
5 *Phalaropus* (g)	3	−0.50	north	−0.50	north
10 *Limnodromus* (g)	2	−1.00	north	−1.00	north
12 Tringini (t)	6	−0.12	—	0.38	south
15 Recurvirostridae (f)	2	1.00	south	1.00	south
$\bar{x}$		0.16	—	0.39	south

[1] g = genus; t = tribe; f = family; so = suborder.

sizes the two-step process of leapfrog migration (seasonal switching and latitudinal segregation), it is unbiased, and it allows the examination of groups containing several species. Most previous examples of interspecific leapfrog migration are of pairs of species chosen haphazardly from multispecies genera (e.g., Lack 1944, Alerstam and Hogstedt 1980). These examples should be reexamined using this new method and using all the species within the genus (or tribe or family or suborder) because it is possible that the species pairs are parts of multispecies leapfrog migration systems.

An investigation of leapfrog migration requires the researcher to set limits for what he will, and will not, consider to be leapfrog migration. Here I consider birds whose degree of seasonal switching is moderate (r values < -0.35), and whose latitudinal overlaps are low (<0.40 on average), to have undergone leapfrog migration. These cutoff points are reasonably conservative, because the classic leapfrog migration example has values of −0.70 and 0.27, respectively.

The underlying assumptions of this method are that the boundaries of the species' ranges are correct and that individuals are evenly (or normally) distributed within the ranges. It is probable that the boundaries only approximate the true boundaries, but it is unlikely that they are so far off as to change the results of these analyses. As for the second assumption, it is certain that within some species the individuals are not evenly distributed within the species' range (e.g., Sanderling, *Calidris alba*; Myers et al. 1985), but it is necessary at present to assume even distribution because only ranges are available for most species. As more information becomes available the details of the method should be changed to allow weighting by relative density.

Because a possible basis for leapfrog migration is the partitioning of latitudes by competitors (Cox 1968), one's definition of which species are likely competitors, will determine at what taxonomic level one is willing to discuss leapfrog migration patterns. Shorebird guilds have not been defined, and whether competition occurs between shorebird species at all is controversial (Duffy et al. 1981, Myers and McCaffery 1984, Puttick 1984). However, there are indications that competition does occur between shorebird species (e.g., Recher 1966, Baker and Baker 1973, Boland 1988) and even between species belonging to different families (e.g., Burger et al. 1979, Pienkowski 1979). It is even possible that all shorebirds (i.e., the suborder Charadrii) should be considered to comprise a single guild.

I believe that if we are to understand leapfrog migration, we need to reveal and study all cases of leapfrog migration, including both intra- and interspecific examples. Until we are certain as to the appropriate taxonomic level, species should be analyzed in groups within genera, tribes, families, and suborders.

Pienkowski et al. (1985), on the other hand, believe that only intraspecific leapfrog migration patterns are "legitimate." They argue that interspecific leapfrog migration is "peripheral to the main argument . . . as the species involved . . . are now ecologically quite distinct . . . ." Certainly more evidence of interspecific competition and latitudinal separation of competitors is needed, but with the evidence that is currently available it is plain that the appeal of these workers to limit leapfrog study to only intraspecific patterns is far too restrictive.

One of the problems associated with leapfrog migration is that there are few examples of the phenomenon. In this study of the North American shorebirds I have found one case of intraspecific leapfrog migration and, at least, four cases of interspecific leapfrog migration. These examples substantially increase the number of known cases of leapfrog migration. Also they come from the first systematic search for leapfrog patterns within any suborder and they show that within this suborder leapfrog migration is common.

An interesting feature of leapfrog migration among these shorebirds is that smaller species tend to leapfrog larger species. This trend is not strong within all leapfrog taxa but it is common enough, and strong enough within some taxa, to warrant further investigation.

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